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EARLIEST TERTIARY EVOLUTION AND RADIATION OF RODENTS IN NORTH AMERICA

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ABSTRACT

All known North American rodents from the late Paleocene and early Eocene are reviewed. Four families are recognized, Ischyromyidae, Sciuravidae, ?Eutypomyidae, and ?Cylindrodontidae. This is the first recognition of the latter two families in the early Eocene. The previously proposed infraorder of rodents, the Franimorpha, is here believed to be composed of members of the Sciuromorpha, and thus does not exist as a distinct taxon.

Five new genera are described, four ischyromyids (*Notoparamys, Quadratomus, Acritoparamys, Apatosciuravus*) and one ?eutypomyid (*Mattimys*), along with eight new species, *Paramys simpsoni, Thisbemys elachistos, Notoparamys arctios, Reithroparamys ctenodactylops, Microparamys reginensis, M. scopaiodon, Apatosciuravus bifax,* and *Franimys ambos.*

Rodents are believed to have originated from an Asian ctenodactyloid-like ancestor rather than a paramyine ancestor, as previously believed. Reithroparamyinae are believed to represent the most primitive ischyromyids, from which the Ischyromyinae and all other subfamilies of the Ischyromyidae can be derived. Ischyromyids do not represent the basal stock from which all later rodents were derived, but may be involved in the ancestry of some later groups of rodents such as the sciurids, eutypomyids, castorids, and the European glirids.

INTRODUCTION

Cope (1877, 1884) was the first to recognize rodents from the early Eocene of North America. He identified three species and referred them to the European genus *Plesiarctomys* Bravard (1850). Two of these species had been described earlier by Leidy (1871) from the middle Eocene, *P. delicatus* and *P. delicatissimus,* and one was new, *P. buccatus.* Loomis (1907) recognized seven new species of *Paramys* Leidy (1871) and one species of *Sciuravus* Marsh (1872) from the "Wasatch" and Wind River Formations of Wyoming. He only questionably accepted Cope's (1877) species *Plesiarctomys*? *buccatus* from the early Eocene of New Mexico.

The only systematic review of early Eocene rodents since Cope's (1884) treatment of all Tertiary mammals of the western United States was by Matthew (1918) as a part of his overall revision with Granger of early Eocene mammals of North America. Matthew (1918) synonymized many of Loomis' species of *Paramys* and introduced two new species, one of *Paramys, P. murinus,* and one of *Mysops* Leidy (1871), *M. kalicola.* Matthew failed, however, to discuss Loomis' (1907) species of *Sciuravus, S. depressus.*

Matthew (1910) and Wilson (1949) discussed early Eocene rodents in their discussions of the early evolution of rodents but offered no major systematic changes. The majority of the new species and systematic reviews of early Eocene rodents have been included in systematic studies of entire faunas (Kelley and Wood, 1954; Gazin, 1952, 1962; Guthrie, 1967, 1971; Rose, 1981) or rodents from a particular fauna (Jepsen, 1937; Gazin, 1961; Wood, 1965). Wood (1962) presented a major review of the "Paramyidae," in which he recognized eight genera and 23 species or subspecies from the early Eocene and latest Paleocene. He did not discuss the early Eocene Sciuravidae or *Mysops kalicola* Matthew (1918) in his review.

All species discussed in this study are from the early Eocene with one species from the latest Paleocene. Granger (1910, 1914) proposed several faunal levels in the early Eocene of North America—Clarkfork, Sand Coulee, Graybull, Lysite, and Lost Cabin (from oldest to youngest). H. E. Wood et al. (1941) proposed the provincial term Wasatchian for the North American early Eocene, and referred Granger's Clarkfork to the latest Paleocene. Van Houten (1945) presented a thorough comparison of the faunas from the Clarkforkian and the Wasatchian. He recognized only three of Granger's faunal levels, Graybull, Lysite, and Lost Cabin, within the Wasatchian and maintained the Clarkforkian as latest Paleocene.

Robinson (1966), in his faunal study of the Huerfano Formation of Colorado, proposed the term Gardnerbuttean for a fourth and uppermost faunal level of the Wasatchian. The Gardnerbuttean was based on the mammalian fauna from the Upper Huerfano Formation.

In a series of papers by workers from the University of Michigan (summarized most recently by Rose, 1981), the Clarkforkian was proposed as representing the earliest Eocene.

The faunal divisions of the early Eocene accepted here are—Graybullian, Lysitean, Lostcabinian, and Gardnerbuttean, as substages of the Wasatchian. The Clarkforkian is accepted here only provisionally as representing the early Eocene, and may be equivalent to the early Graybullian of Van Houten (1945).

Because rodents have been used, at least in part, in separating different faunal levels of the early Eocene and latest Paleocene (Van Houten, 1945; Robinson, 1966; Guthrie, 1971; Rose, 1981) and no overall systematic review of these rodents has been presented for over 60 years (Matthew, 1918), a reexamination of the systematics of this group of mammals is necessary.

Tooth nomenclature used in discussion is after Wood and Wilson (1936). All dental measurements are in millimeters.

Abbreviations used: ACM—Pratt Museum, Amherst College; AMNH—American Museum of Natural History; CM—Carnegie Museum of Natural History; CU—University of Colorado Museum of Geology; FMNH—Field Museum of Natural History; KU—University of Kansas Natural History Museum; MCZ—Museum of Comparative Zoology, Harvard University; PU—Princton University; ROM—Royal Ontario Museum; TMM—Texas Memorial Museum; TTM—Museum of Texas Tech University; UCMP—University of California Museum of Paleontology; UMMP—University of Michigan Museum of Paleontology; USNM—U.S. National Museum of Natural History; UW—University of Wyoming Museum of Geology; WAM—Webb School, Alf Museum; YPM—Yale Peabody Museum; N—number of specimens; M—mean; S—standard deviation; V—coefficient of variation; OR—observed range; a-p—anteroposterior length; tra—anterior transverse width; trp—posterior transverse width.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Suborder Sciuromorpha Brandt, 1855

Discussion.—In his 1955 classification, Wood included the primitive ischyromyoid rodents (paramyids, ischyromyids, cylindrodontids, sciuravids, protoptychids, and phiomyids) in the suborder Sciuromorpha, one of Brandt's (1855) original three suborders which also included the sciurids and aplodontids. Later, Wood (1937, 1958, 1962) included the ischyromyoids in the Protrogomorpha of Zittel (1893) along with the aplodontoids. In a classification of the Ischyromyidae (including Wood's Paramyidae), Black (1971) included the family in the Sciuromorpha without discussion. Sciuromorpha is used here in the same sense as it was by Wood (1955) with the exclusion of Phiomyidae.

Wood (1975) revised his classification of rodents and accepted the two-fold subordinal division of the rodents proposed by Tullberg (1899)—Hystricognathi and Sciurognathi. He (Wood, 1975) erected a new infraorder Franimorpha based predominantly on the presence of an "incipiently" hystricognathous mandible, and included the Reithroparamyinae (*sensu* Wood, 1962), *Prolapsus* Wood (1973), *Protoptychus* Scott (1895), and *Guanajuatomys* Black and Stephens (1973) in the Franimorpha. Later, the Cylindrodontidae were also included in the Franimorpha (Wood, 1980, 1981).

Wood (1975) included the Paramyidae (excluding the Reithroparamyinae) in the infraorder Protrogomorpha of the suborder Sciurognathi, while maintaining the Reithroparamyinae as a subfamily of the Paramyidae. Finally, he (Wood, 1981) raised the Reithroparamyinae to the family level to avoid the ambiguity of having a single family in two different suborders.

None of the species included in the Franimorpha (Wood, 1975, 1980) appear to have attained hystricognathy as defined by Tullberg (1899). The holotype of *Franimys amherstensis,* the species on which the infraorder is based, includes the posterior half of a right mandible without teeth (ACM 10524). This specimen, however, is badly broken and calcite has filled and expanded many of the cracks distorting the shape of the mandible (Fig. 20), thus making it impossible to determine the original position of the angle. The only referred mandible of *F. amherstensis* (ROM 2180) identified by Wood (1962) is sciurognathous. This specimen, however, is not *F. amherstensis* and is referred below to *Acritoparamys atwateri* (Loomis, 1907).

Dawson (1977) noted that the mandible of *Reithroparamys,* considered hystricognathous by Wood (1962), was fully sciurognathous and not "incipiently" hystricognathous. In other members of Wood's (1962) Reithroparamyinae, the incipient or subhystricognathy is truly sciurognathy. The angle of the mandible is not positioned lateral to the horizontal ramus as in true hystricognathous rodents. The mandible of these species differs from that of *Paramys* by having the masseteric fossa bounded by much heavier ridges and terminating more anteriorly on the side of the mandible. This same effect of "incipient hystricognathy" is as strong on sciuravids and manitshine ischyromyids for the same reasons. In some instances the presence of a heavy chin process enhances a groove visible on the ventral side of the mandible which has been confused with the groove for the *masseter superficialis pars reflexus deep* on the ventral side of the mandible in truly hystricoganthous rodents (Woods, 1972).

Black and Stephens (1973) described the mandible of *Guanajuatomys* from Mexico as being hystricognathous. The angle of this mandible, however, is not laterally displaced from the plane of the horizontal ramus, and the mandible should not be considered hystricognathous.

The late Eocene rodent *Protoptychus* (Scott, 1895; Wilson, 1937) is fully hystricomorphous (Wahlert, 1973). Though the mandible of *Protoptychus* has not been fully described, Wahlert (1973), based on a personal communication from W. Turnbull, stated that *Protoptychus* was fully hystricognathous. This observation was followed by several authors (for example Wood, 1975; Dawson, 1977). However, more complete and fully prepared undescribed material of *Protoptychus* now available shows that the complete mandibles of *Protoptychus* are clearly sciurognathous.

Several mandibles of the cylindrodont *Mysops* from the middle Eocene are present in the collections of the USNM. None of the specimens that preserve the mandibluar angle are hystricognathous. Early Oligocene cylindrodonts have a mandible similar to those of reithroparamyines and are not hystricognathous.

The type specimen of *Prolapsus sibelatoris* (TMM 41372-179) is not fully hystricognathous jaw as stated by Wood (1972, 1973). The angle of the mandible of *Prolapsus* is no more laterally displaced than that of the early Eocene sciuravid *Knightomys* Gazin (1961). The mandible of *Prolapsus* is very robust and the breadth of the mandible is much greater than that of *Knightomys*, making the angle look more laterally displaced. Wood (1977, 1981) also stated that the skull of *Prolapsus* was hystricomorphous. However, the undescribed skull of *Prolapsus* on which Wood based his statement has been examined and compared to the skull of Bridgerian *Sciuravus*. The infraorbital foramina of these two genera are the same relative size and are clearly protrogomorphous.

Wood (1975) also noted that a small fossa on the lateral side of the mandible just ventral and posterior to the condyle of some franimorphs was for the attachment of the *masseter lateralis profundus pars posterior deep*, a muscle unique to hystricognathous rodents (Woods, 1972). Other than in the hystricognathous rodents and some "franimorphs," Wood (1975) found this fossa in the Oligocene sciuromorphous *Eutypomys*. This small fossa is also present in all manitshines, "*Leptotomus*" *costilloi*, and *Paramys copei*, all of which are ischyromyids. Whether or not it housed the attachment of this muscle cannot be determined, but clearly this feature cannot be used to relate the "franimorphs" to later hystricognathous rodents.

The "incipiently hystricognathous" condition in some early ischyromyids and sciuravids noted by Wood (1962, 1973, 1975) appears to be more common among early rodents than not, and may represent the primitive condition in rodents. Landry (1957:83), the first to suggest this hypothesis, stated, "It therefore seems that the most primitive ischyromyids have a jaw angle which shared the features of both Hystricognathi and Sciurognathi and which could have been the kind of structure possessed by their common ancestor."

In all, no specimens in the "Franimorpha" possess a definitely hystricognathous mandible. The Reithroparamyidae (Wood, 1981) should be returned to the subfamilial level under the Ischyromyidae. *Prolapsus* should be included as a member of the Sciuravidae. *Protoptychus* is unique among Eocene rodents and is best maintained in its own family Protoptychidae (see Simpson, 1945; Wilson, 1949). *Guanajuatomys* cannot be readily referred to any existing family of rodents, and is best maintained as Family *insertae sedis*.

Family Ischyromyidae Alston, 1876

Discussion.—A great deal of discussion has been concerned with the composition of the Ischyromyidae (Black, 1968*a*, 1971; Wood, 1976*a*). Here, the Ischyromyidae will include the "Paramyidae" of Miller and Gidley (1918) and Wood (1962) as a subfamily (or subfamilies) of the Ischyromidae. The differences between *Ischyromys* and the "Paramyidae" cited by Wood (1976*a*) are mainly concerned with the attachment of the masseter muscle on the skull. This difference is not significant enough to establish two distinct families for obviously closely allied genera (Black, 1968*a*, 1971). Black's (1971) diagnosis of the Ischyromyidae is accepted here.

Subfamily Paramyinae Simpson, 1941*b*

Diagnosis.—Medium to large sized rodents; skull with robust rostrum; nasal bones extend posteriorly on the skull far beyond the posterior extent of the premaxillaries; interparietal not present; auditory bulla not coosified with the skull; cheek teeth with simple pattern; P^4 submolariform and lacking a hypocone on all but the most primitive species; protoloph and metaloph more nearly parallel on upper molars; hypocone on upper molars usually small; anterior cingulum on lower molars continuous with metaconid and protoconid; mesoconids usually absent; entoconids generally continuous with posterolophids.

Tribe Paramyini, new rank

Diagnosis.—Medium sized paramyines; mandible intermediate in depth; lower incisors relatively narrow and flattened or convex anteriorly; cheek teeth distinctly cuspate; masseteric scar on mandible ends anteriorly below the M_2–M_3 boundary; posterior margin of the anterior root of the zygoma level with the posterior margin of P^4.

Included genera.—*Paramys* Leidy (1871), *Leptotomus* Matthew (1910), *Rapamys* Wilson (1940), *Thisbemys* Wood (1959*a*), *Uriscus* Wood (1962), *Hulgana* Dawson (1968*a*), and *Notoparamys,* new genus.

Comparison.—Paramyini differ from all reithroparamyines and ischyromyines by the lack of a hypocone on P^4; position of the anterior root of the zygoma and masseteric fossa on the mandible; having nasal bones extend farther posterior than the premaxillaries; lacking an interparietal bone on the skull; and generally having the entoconid continuous with the posteriolophid on the lower cheek teeth; and M^2 being longer than M^1 lingually. The Paramyini also differ from the Pseudoparamyinae and Ailuravinae by the lack of postorbital processes on the skull and having the nasal bones extending posterior to the premaxillary bones. The Paramyini are also generally larger than reithroparamyines.

The Paramyini can only be separated from the Manitshini by their smaller size and more cuspate cheek teeth. In manitshines the cheek teeth have shallow, nearly flat basins, and the cusps are marginal and less distinct. The skull and mandible of Paramyini are much more slender than in the Manitshini.

Paramys Leidy, 1871

Type species.—*Paramys delicatus* Leity, 1871.

Paramys copei Loomis, 1907

Plesiarctomys delicatissimus (Leidy) Cope, 1877, in part.
Paramys copei Loomis, 1907.
Paramys major Loomis, 1907.
Paramys primaevus Loomis, 1907.
Paramys quadratus Loomis, 1907.
Paramys bicuspis Loomis, 1907.
Paramys copei bicuspis Loomis, Wood, 1962.
Paramys copei major Loomis, Wood, 1962.

Type specimen.—AMNH 4755, skull and mandibles with some postcranial bones.

Horizon and locality.—Type and some referred specimens from type area of Lost Cabin Member, Wind River Formation, Wyoming. Other referred specimens from the Lysite Member, Wind River Formation; Debeque Formation, Colorado; Huerfano Formation, Colorado; Willwood Formation Wyoming; and San Jose Formation, New Mexico.

Age.—Early Eocene (Clarkforkian through Gardnerbuttean).

Referred specimens.—CM 19899, 19901, 9930, 20892, 21147–21150, 21168, 21170, 21172–21174, 21176–21178, 21180, 21181, 21218, 21227, 21934–21937, 21945, 22161–22167, 22169–22171, 22173, 22174, 22177, 22179, 22181–22203, 22204–22206, 22209, 22210, 22213, 22215, 22219, 22535, 22545, 22546, 22599, 22828, 22932–22934, 26509, 26513, 28711, 29160–29163, 30596, 30598, 31016, 35849–35857, 35864, 36495, 36496, 36498, 36500–36508, 36923–36926, 37165, 37171, 37177–37185, 38739, 38740, 4955 (from Lost Cabin Member, Wind River Formation).

CM 19894, 19895, 20888, 21899, 21913, 22820, 22821, 22822, 22824, 22825, 22830, 22832, 22834, 22838, 22846, 22880, 28706–28710, 28742, 28935, 29185, 35009–35014, 35016, 35017, 35028, 35031, 35032, 35926, 35933, 35935, 35936, 36085, 36087, 36088, 37077–37086, 38742, 38743, 38746–38756 (from Lysite Member, Wind River Formation).

CM 38757–38760 (from Almagre Member, San Jose Formation).

CM 38764 (from Largo Member, San Jose Formation).

CM 12006, 12008, 36116, 36256 (from Willwood Formation).

Also see Wood (1962:255–256) for referred material from other localities.

Discussion.—Loomis (1907) recognized seven species of *Paramys* from the early Eocene. Matthew (1910), in his review of the Ischyromyidae, recognized all of Loomis' species and included *Paramys buccatus* (Cope, 1877) from the early Eocene of New Mexico. Matthew (1910) divided the early Eocene *Paramys* species into three separate groups, the *P. buccatus* group (including *P. buccatus* and *P. atwateri*), the *P. primaevus* group (including *P. primaevus, P. excavatus, P. quadratus,* and *P. major*), and the *P. delicatus* group (including *P. copei, P. bicuspis,* and the Bridgerian species of *Paramys*).

Later, Matthew (1918) recognized only five early Eocene species of *Paramys,* synonymizing *P. primaevus* and *P. bicuspis* with *P. copei,* and allocating *P. quadratus* to a subspecies of *P. major.* Matthew did not discuss his earlier groupings of the species of *Paramys.*

The next major review of *Paramys* was by Wood (1962), who synonymized Loomis' (1907) *P. primaevus, P. quadratus, P. major,* and *P. bicuspis* under *P. copei,* recognizing *P. major* and *P. bicuspis* as subspecies. Wood followed Matthew (1910) in arranging species groups of *Paramys.* He included *P. copei* in a *P. delicatus* group along with the two Bridgerian species (*P. delicatus* and *P. delicatior*) and a new Wasatchian species *P. wortmani.*

Wood's (1962) overall synonymy of Loomis' species under *P. copei* is accepted here. His subspecific assignments cannot, however, be substantiated. The characters used by Wood (1962) to identify the subspecies of *P. copei* (incisor shape, size, shape of the mesostyle on the upper molars) are only minor variations within the range of variation of a single population. In many areas (for example, the Wind River Basin, Bighorn Basin, and Debeque Formation) as many as all three subspecies are recognized from the same level. This common occurrence and overlap of diagnostic characters seems to indicate that only a single species is present in all of these areas.

Guthrie (1971) synonymized *Paramys wortmani* Wood (1962) and specimens referred by Wood to *Thisbemys perditus* from the Lost Cabin Member, Wind River Formation with *P. copei. Paramys wortmani* is clearly distinct from *P. copei* and referred below to *Mytonomys* on the basis of a newly discovered maxillary fragment. The sample of *T. perditus* identified by Wood (1962) from Lost Cabin are all specimens in his private collection (labelled AEW) and appear from the figures to be some specimens of *P. copei* as well as specimens of *P. excavatus.*

Rose (1918) referred a few isolated upper incisors from the Clarkforkian of the Bighorn Basin to *Paramys* cf. *excavatus.* He noted that these incisors were markedly larger than those of *P. excavatus,* but that the lower dentitions referred to this species were near the size of *P. excavatus taurus* Wood (1962). The isolated upper incisors referred by Rose (1981) to *P.* cf. *excavatus* do not appear to be referable to *P. excavatus,* but more nearly approach *P. copei* or *Franimys amherstensis* in size. These specimens are longer anteroposteriorly than any specimens of *P. copei* (see Wood, 1962: Tables 9, 11, 13; Guthrie, 1967: Table 12; Rose, 1981). However, the single I^1 figured by Rose (1981: Fig. 64), according to the scale given on the illustration, is anteroposteriorly shorter than any of the measurements given by Rose for I^1 and well within the range of *P. copei* or *F. amherstensis.* This discrepancy in measurements may be due to the fact that Rose measured the length along the wear surface as opposed to the shortest anteroposterior diameter of the tooth.

These I^1s reported by Rose (1981) are here referred to *P. copei.* While these specimens are the same size as I^1 of *F. amherstensis,* enamel extends farther posteriorly on the medial side of the tooth as in *P. copei.* The rare occurrence of *P. copei* in the Clarkforkian is also true for the early Wasatchian levels in the Bighorn Basin.

Wood (1962) provided adequate figures of *P. copei.* Measurements of *P. copei* are provided by Wood (1962: Tables 8–13) and Guthrie (1967: Table 12; 1971: Tables 15, 18).

Wood's (1962) species groups of *Paramys* included the *P. delicatus* group (mentioned above) and a second group, the *P. excavatus* group which included *P. atavus, P. francesi, P. huerfanensis,* and the European species *P. teilhardi.* These species groupings appear somewhat artificial. The only feature that unites the species in each group is size, the *P. delicatus* group species being larger, and the *P. excavatus* group species, smaller. All of the species included in Wood's *P. excavatus* species group are referable to other genera, except *P. excavatus* (see Michaux, 1964; and later discussion this paper).

No species groups are recognizable within *Paramys.* This genus is composed of several distinct species that cannot be grouped into any category other than species.

Paramys excavatus Loomis, 1907
(Fig. 1)

Paramys excavatus Loomis, 1907.
Franimys lysitensis Guthrie, 1967.

Type specimen.—ACM 327, right mandible with M_1–M_3 and partial P_4.

Horizon and locality.—Type and some referred specimens from the type area of Lysite Member, Wind River Formation, Wyoming. Other referred material from the Debeque Formation, Colorado; Knight Member, Wasatch Formation, Wyoming; Lower Huerfano Formation, Colorado; Lost Cabin Member, Wind River Formation, Wyoming; and Almagre Member, San Jose Formation, New Mexico.

Age.—Middle early Eocene (Lysitean to Lostcabinian).

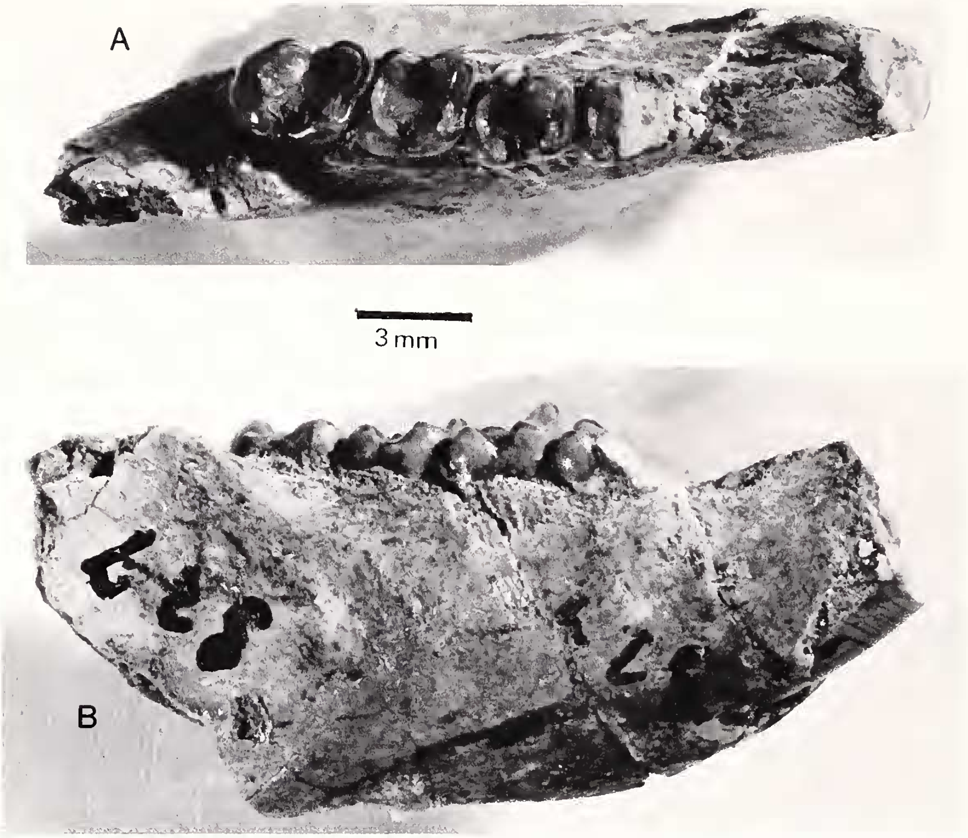


Fig. 1.—Holotype of *Paramys excavatus,* ACM 327. A) Occlusal view of P$_4$ (part)–M$_3$. B) Lateral veiw of mandible.

Referred specimens.—CM 21179, 22211, 22212, 22214, 22216, 22217, 22218, 22220, 22922, 26520, 31333, 35858, 36497, 37168, 37174, (from Lost Cabin Member, Wind River Formation).

CM 19893, 22853, 28705, 35029, 35030, 35934, 37090, 37092 (from Lysite Member, Wind River Formation).

CM 38761 (from Almagre Member, San Jose Formation).

CM 19540 (from Lower Huerfano Formation, locality VI).

Also see Wood (1962:256) for referred specimens from other areas.

Emended diagnosis.—Small species; enamel on lower molars smooth; lower molars nearly square in occlusal outline; P^4 anteroposteriorly compressed, lacking a protoconule and hypocone.

Discussion.—Wood (1962) recognized four subspecies of *P. excavatus.* This species is here restricted to his *P. e. excavatus.* The remaining subspecies of *P. excavatus* are referred elsewhere and will be discussed in following sections.

A single lower jaw with P$_4$–M$_3$ (CM 19540) from the Lower Huerfano (locality VI, Robinson, 1966) is referable to *P. excavatus.* This species has previously not been reported from the Huerfano (Wood, 1962; Robinson, 1966). A specimen of *P. excavatus* is now also known from the Almagre Member of the San Jose Formation of New Mexico (CM 38761).

Franimys lysitensis was described by Guthrie (1967:27) as differing from *P. excavatus* in ". . . weakness of the mesostylid and the anterior cingulum, and in the indistinctness of the trigonid basin." Guthrie's type (ACM 2536) and referred specimens (ACM 4394) do not differ markedly from the type and referred material of *P. excavatus,* and *F. lysitensis* should be considered a junior synonym of *P. excavatus.*

Guthrie (1971) synonymized both *Reithroparamys atwateri* and *R. pattersoni* with *P. excavatus.* The two specimens referred by Wood (1962:135) to *R. pattersoni* from the type area of the Lost Cabin Member of the Wind River Formation are more likely referable to *P. copei.* However, the remainder of the hypodigm for *R. pattersoni* from the Debeque Formation of Colorado is clearly distinct from *Paramys* (see below discussion of *Acritoparamys pat-*

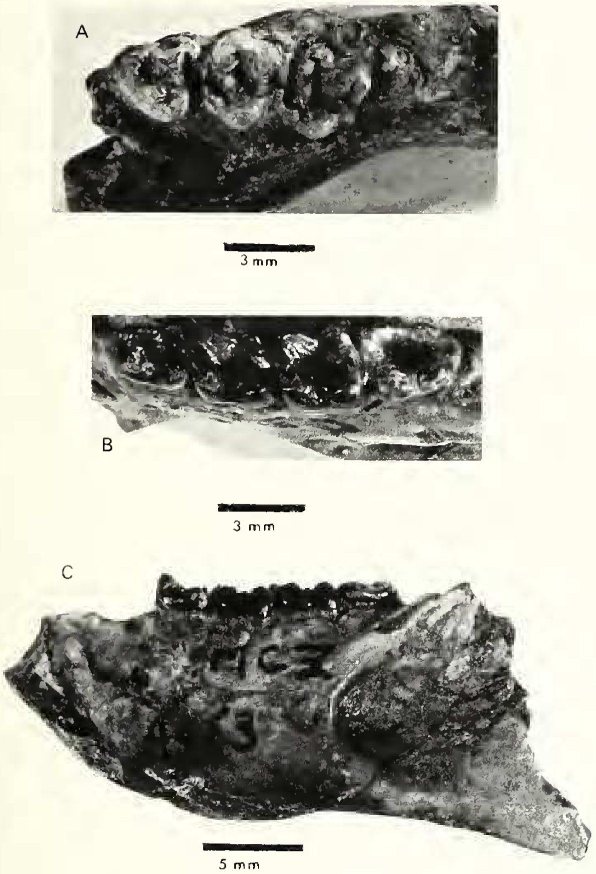


Fig. 2.—Upper and lower dentitions of *Paramys taurus.* A) RP^4–M^3, CM 12223. B) LP$_4$–M$_3$, MCZ 4463 (type). C) Lateral view of mandible, MCZ 4463.

tersoni). Likewise *R. atwateri* is also distinct from *P. excavatus* and should not be considered a synonym (see discussion of *A. atwateri*).

Dental measurements for *P. excavatus* were provided by Wood (1962: Tables 14, 15) and Guthrie (1967: Table 13; 1971: Table 16).

Paramys taurus Wood, 1962, new rank
(Fig. 2, Table 1)

Paramys excavatus taurus Wood, 1962.
Paramys excavatus obliquidens Wood, 1962.

Type specimen.—MCZ 4463, both mandibles with LP$_4$–M$_3$ and RM$_1$–M$_3$.

Horizon and locality.—Type from "1.7 miles west of Wardell's Lake, east of Tatman Mountain" (Wood, 1962:56), Willwood Formation, Wyoming. Referred specimens from elsewhere in the Willwood Formation and Four Mile Fauna, Wasatch Formation, Colorado.

Age.—Earliest Eocene (Clarkforkian to Graybullian).

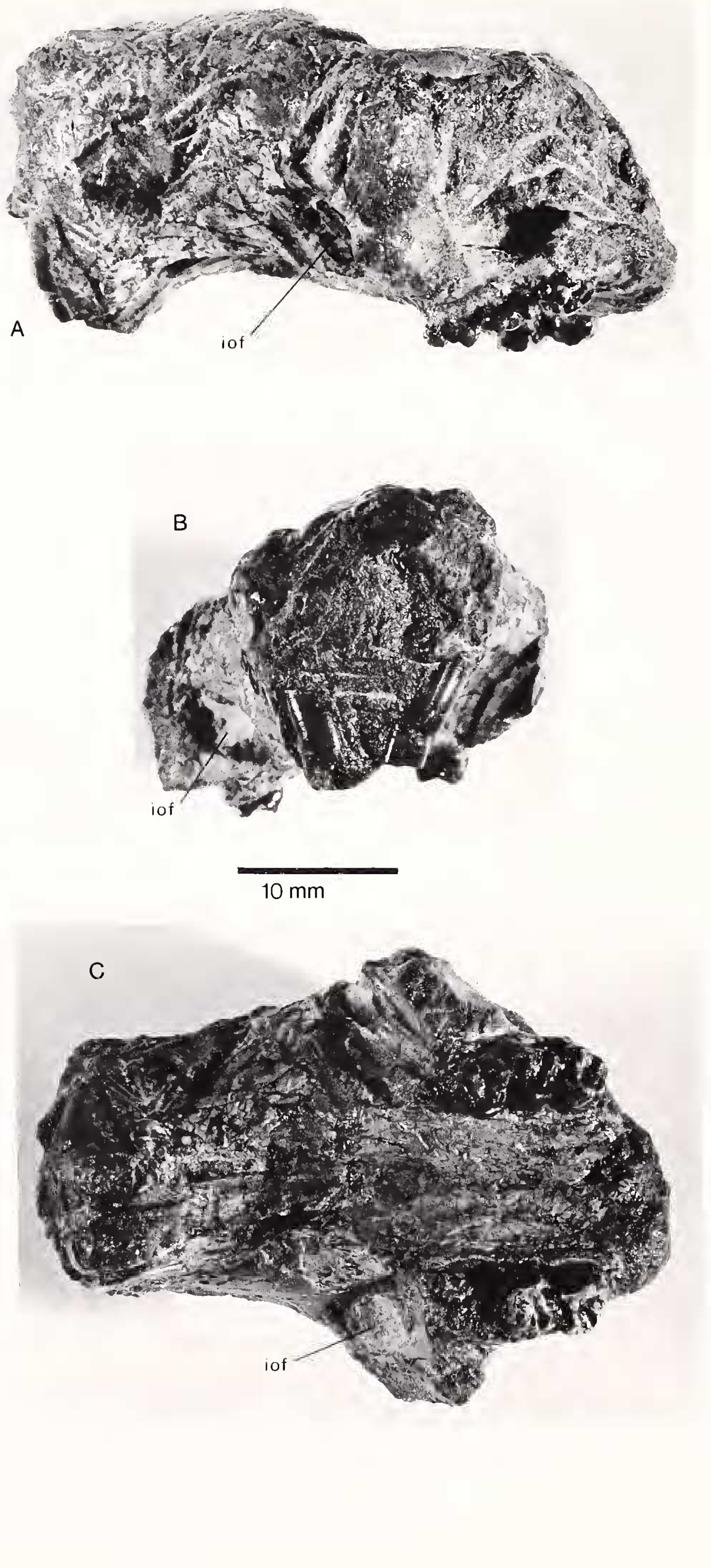
Referred specimens.—CM 12223, maxilla with P^4–M^3 from the Willwood Formation and several hundred isolated teeth from Sand and East Alheit Pocket Quarries, Four Mile fauna, Moffett County, Colorado (unnumbered AMNH specimens). Also see Wood (1962:58, 256) for total hypodigm.

Emended diagnosis.—Small species; lower molars rhomboidal in occlusal outline; hypoconulid variably present on P$_4$–M$_2$ which disappears with wear; P^4 anteroposteriorly compressed with protoconule and hypocone minute to absent.

Discussion.—Wood (1962) separated *P. excavatus taurus* from *P. e. obliquidens* on the basis of minor morphological differences of the molars and incisor, although these subspecies were of equal size and from the same levels of the Willwood Formation, Bighorn Basin, Wyoming. He stated that *P. e. obliquidens* had an I$_1$ with a concave anterior surface and a minor ridge running from the hypoconid toward the entoconid on the lower molars, not seen in *P. e. taurus.* The I$_1$ of the holotype of *P. e. obliquidens* (AMNH 16970) is not concave as figured by Wood (1962: Fig. 18p). The tooth appears flat anteriorly. The groove on the surface of I$_1$, if it were

Table 1.—*Dental measurements of* Paramys taurus, Paramys simpsoni, *and* Paramys nini. *Measurements in millimeters.*

Specimen no.	P^4			M^1			M^2			M^3	
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra
					Paramys taurus						
CM 12223	2.23	2.93	—	2.78	3.32	3.27	2.83	—	—	2.89	3.02
					Paramys simpsoni						
AMNH 80739 L	3.06	3.53	3.68	3.28	3.60	3.55	—	3.74	—	—	—
AMNH 80739 R	—	—	—	3.19	3.73	3.62	—	3.79	—	—	—
					Paramys nini						
YPM 14410 L	3.01	3.83	3.96	3.32	3.48	3.51	3.27	3.55	3.31	3.68	3.35
YPM 14410 R	—	—	—	3.35	3.50	3.22	—	—	—	—	—


A
iof
B
iof
10 mm
C
iof

truly concave, is so shallow that it is hardly detectable. The differences in the cross-sectional shape of I_1 of *P. e. taurus* and *P. e. obliquidens* are very slight and are no more different than variations accepted by Wood for other species of *Paramys.*

The minute ridge running from the hypoconid in *P. e. obliquidens* is only a minor crenulation on the enamel surface of the molars, and is equally as distinct in specimens of *P. e. taurus.* No differences exist between *P. e. obliquidens* and *P. e. taurus.* Therefore, they should be considered a single species that is distinct from *P. excavatus.*

Wood (1962: Fig. 18g) noted and figured a ridge extending into the talonid basin from the entoconid of P_4 on the type of *P. e. taurus.* This feature does not occur on the type (MCZ 4463) and cannot be considered a character of this species.

Paramys taurus is distinct from *P. excavatus* in having: 1) more rhomboidal shaped lower molars; 2) larger mesoconid; 3) a hypoconulid on the lower molars; and 4) minute hypocone generally present on P^4. These differences are consistent in all specimens referable to *P. taurus* and are distinct enough to warrant considering *P. taurus* as a separate species.

Wood (1962) stated that *P. e. obliquidens* (=*P. taurus*) was so close to *Reithroparamys atwateri* that he was tempted to put the subspecies in both *Paramys* and *Reithroparamys. Paramys taurus,* however, differs from *R. atwateri* in being larger with less distinct, more lingually placed hypoconulid on the lower molars; posteroloph continuous with the entoconid; and an accessory mental foramen only variably present on the mandible in differing positions. *Paramys taurus,* though similar in many features to *R. atwateri,* is clearly distinct from it.

A maxilla (CM 12223) with P^4–M^3 recovered from the Gray Bull level in the Bighorn Basin approaches the size of *P. taurus.* The molars are similar to those of *P. excavatus* and P^4 is anteroposteriorly compressed as in *P. excavatus* and *P. copei.* Several unnumbered isolated teeth are present in the Four Mile fauna (see McKenna, 1960). They are chiefly divisible into two species, *P. taurus* and "*R.*" *atwateri,* and are separable on the characters listed above. A number of specimens from the Bighorn Basin of *P. taurus* are being described elsewhere by T. Bown of the United States Geological Survey. Among these specimens there are some upper dentitions with P^4. A hypocone is only variably present on these specimens.

The three specimens of upper dentitions referred by Wood (1962) to *P. e. taurus* are disproportionately small relative to the known lower dentitions. (AMNH 15710 has been remeasured in Table 6, this paper). These specimens also differ from *P. taurus* in having P^4 not anteroposteriorly compressed with a distinct protoconule, anterior root of the zygoma level with the center of P^4, hypocone on M^1–M^2 larger in relation to the protocone, and and the protoloph and metaloph are less parallel converging toward the protocone. All of these features are characteristic of reithroparamyines. Thus, the three specimens of upper dentition referred by Wood to *P. e. taurus* should be referred to *R. atwateri,* which is known from the same localities of *P. taurus.*

The lower dentitions of "*Paramys* cf. *excavatus*" from the Clarkforkian of the Bighorn Basin (Rose, 1981) were described as being smaller than those of *P. e. taurus* from the early Wasatchian. However, only one specimen of Rose's "*P.* cf. *excavatus*" (UMMP 65117) is smaller than the ranges measured for *P. taurus* (including *P. e. obliquidens*) by Wood (1962: Tables 16 and 18). Only two measurements on UMMP 65117 (anteroposterior length of P_4, anterior width of M_3) are outside of the size range for *P. taurus.* The teeth of UMMP 65117 are so heavily worn that enamel has been lost on the lateral sides of the teeth and the anterior face of P_4, thus obscuring the true length and/or width of the teeth. The smaller size of this specimen of "*Paramys* cf. *excavatus*" can only be viewed as an effect of the wear of the teeth. Hence, the Clarkforkian specimens referred to this species are here allocated to *P. taurus* (see Wood, 1962: Tables 16, 18, for measurements of *P. taurus*).

***Paramys simpsoni,* new species**
(Figs. 3, 4b, Table 1)

Type specimen.—AMNN 80739, partial skull with upper incisors and LP^4–M^2, RM^1–M^2.

Horizon and locality.—Locality 150 (Simpson, 1948), Largo Member, San Jose Formation, New Mexico.

←

Fig. 3.—Skull of *Paramys simpsoni,* AMNH 80739 (type). A) Lateral view. B) Anterior view. C) Ventral view. (iof = infraorbital foramen).

Age.—Middle or late early Eocene (Lysitean or Lostcabinian).

Hypodigm.—Type only.

Diagnosis.—Equal in size to *Paramys copei*; I^1 with narrow central groove; P^4 with large paracone which expands at the tooth anteriorly; P^4 with shortest (anteroposterior) length at the buccolingual center of the tooth; infraorbital foramen large for ischyromyid; maxillary-premaxillary suture on the side of the rostrum bends farther anterior than in *P. copei*; upper molars as in *P. copei*.

Etymology.—Patronym for George G. Simpson, who recovered the holotype.

Description.—In size and general shape, AMNH 80739 does not differ from *P. copei*. The posterior margin of the anterior root of the zygoma is in line with the anterior cingulum of M^1. The maxillary-premaxillary suture on the side of the snout is similar to that of *P. copei* but extends farther anteriorly. The infraorbital foramen is larger than in any other Eocene ischyromyid. It is evident on the specimen that preparation has somewhat altered the shape of the infraorbital foramen, but the true size of the foramen does not appear to have been affected.

A distinct groove is present on the anterior face of the upper incisors. P^4 is smaller than M^1, has a double metaconule, a large mesostyle with a low, short extension into the central basin, and lacks a hypocone. The posterior cingulum bends lingually at the posterolingual corner of the tooth. The paracone is more anteriorly placed than in P^4 of *P. copei* and slightly lingual to the metacone, making the tooth much longer bucally than lingually. The shortest anteroposterior length of P^4 is at the center of the tooth giving the tooth an "hourglass" occlusal shape. The anterior cingulum runs from the buccal margin of the protocone to the level of the center of the paracone. The protoloph is low with a minute protoconule.

The hypocone on the molars is small. M^1 is longer buccally than in *P. copei*, but not beyond the range of variation for that species. In all other features of the molars, *P. simpsoni* is similar to *P. copei*.

Discussion.—The size of the infraorbital foramen and distinct groove on the upper incisors of AMNH 80739 are unique for any species of *Paramys*, although in size and morphology of the molars *P. simpsoni* is identical to *P. copei*. Other features that separate *P. simpsoni* from *P. copei* are the morphology of P^4 and the pattern of the maxillary-premaxillary suture on the lateral side of the snout.

Several species of paramyines have been reported as having a shallow sulcus on the lower incisor (see Wood, 1962). This character is almost always variable when present. No upper incisors of *Paramys* are known to be sulcate. Only two ischyromyids are known to have a central groove on the upper incisor, *Reithroparamys delicatissimus* and "*Leptotomus*" *sciuroides*. Wood (1962) assigned an isolated upper incisor with a central groove to *Leptotomus* (=*Tapomys*) *tapensis* but its reference is uncertain. *Leptotomus bridgerensis* is known to have sulcate upper incisors but each incisor has two very broad, shallow grooves, unlike *P. simpsoni*. The groove in the I^1 of *R. delicatissimus* and "*L.*" *sciuroides* are also broader than that in I^1 of *P. simpsoni*.

There is no indication that a groove in the upper incisor is a variable character in paramyines. However, so few associated upper incisors are known that it is practically impossible to check at this time.

There is no indication that the infraorbital foramen of *P. simpsoni* has been invaded by a branch of the masseter muscle, though this foramen is clearly larger than in any other Eocene ischyromyid. It is difficult to base a new genus on *P. simpsoni* because it cannot be determined whether or not some of the characteristic features (sulcate I^1, enlarged infraorbital foramen, premaxillary-maxillary suture pattern) are just minor variations within a single genus or not. If more specimens referable to this taxon can be recovered, and these characteristics can be shown to be consistently different from those of *Paramys*, *P. simpsoni* may be distinct enough to warrant establishing a new genus of paramyine.

Paramys nini (Wood, 1962)
(Fig. 4a, Table 1)

Thisbemys nini Wood, 1962.

Type specimen.—YPM 14410, partial skull with RP^4–M^2 and LP^4–M^3.

Horizon and locality.—Head of Govilan Arroyo, Largo Member, San Jose Formation, New Mexico.

Age.—Middle early Eocene (Lysitean or Lostcabinian).

Emended diagnosis.—Intermediate sized species of *Paramys*; P^4 larger than M^1 with distinct hypocone; multiple mesostyles on upper cheek teeth; M^3 elongate posteriorly.

Discussion.—In the original description, Wood (1962) included the holotype from New Mexico and several referred specimens from the Huerfano Formation in the hypodigm of *Thisbemys nini*. All of the referred specimens are here allocated to *T. perditus* (see discussion below of *T. perditus*), making the holotype the only known specimen of the species.

Wood (1962) noted that the crenulations of the tooth enamel on the molars of *T. nini* were of a nature different from those of other species of *Thisbemys*, but maintained it in the genus. The crenulations on the cheek teeth of the holotype of *Para-*

mys nini are limited to the mesostylar area, and merely represent multiple mesostyles, a character common also in many specimens of *P. copei.* Both P^4 and M^1 of *P. nini* have a buccolingually elongate mesostyle which is larger than any of the other minute mesostyles on the teeth. Other than the elongate mesostyle, there is virtually no wrinkling of the enamel beyond that visible in those of other species of *Paramys.*

As noted by Wood (1962) the P^4 of *P. nini* is quite large relative to M^1, and M^3 is slightly more expanded posteriorly than in *P. copei.* It is difficult to determine whether or not the expansion of M^3 of YPM 14410 (type of *P. nini*) is truly distinct because M^3 is quite variable in most Eocene rodents, and the difference in *P. nini* is so slight it might well be within the bounds of variation for *P. copei.* P^4 of *P. nini* is distinct from that of any other species of *Paramys* in being wider than M^1 and having a hypocone. P^4 of *P. nini* is more molariform than that of *P. taurus,* which is the only other species of *Paramys* to possess a hypocone on P^4. The hypocone of P^4 of *P. nini* is very closely appressed to the protocone and separated from it only by a shallow groove. There is no groove separating the protocone from the hypocone and the lingual wall of the tooth as in the molars, thus, it appears that after moderate wear the hypocone would be indistinguishable from the protocone.

YPM 14410 is nearly identical to the holotype of *P. copei* (AMNH 4755) in size and all features of the skull that can be observed. The upper incisors and M^1–M^2 are also nearly identical to those of *P. copei.* M^1 of *P. nini* is slightly longer anteroposteriorly than in *P. copei,* but has the same proportions as M^1 in the skull described above of *P. simpsoni.*

Three skulls of *Paramys* are known from the Largo Member of the San Jose Formation of New Mexico, *P. copei* (CM 38764), *P. simpsoni* (AMNH 80739), and *P. nini* (YPM 14410). These skulls are all nearly identical in size and morphology of the upper molars. The major difference between them is the morphology of P^4. There are no known lower dentitions of appropriate size to be referred to these species from the Largo of New Mexico.

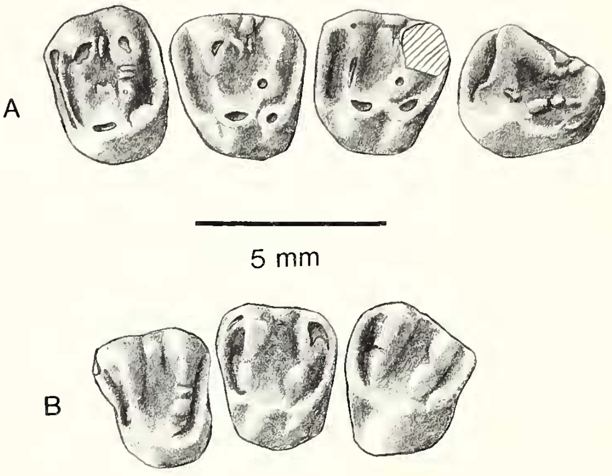


Fig. 4.—Upper cheek teeth of *Paramys nini* and *P. simpsoni.* A) *P. nini,* LP^4–M^3, YPM 14410 (type). B) *P. simpsoni,* LP^4–M^2, AMNH 80739 (type).

The morphology of P^4 of *Paramys nini* more closely approaches that of the Bridgerian species *P. delicatus* than does that of any other early Eocene species. *Paramys copei, P. excavatus* and *P. taurus* have a relatively short and wide P^4 that tapers lingually with a reduced protoloph and minute to absent protoconule. Both *P. nini* and *P. delicatus* have a longer, more molariform P^4 that is more nearly square in occlusal outline. The holotype of *P. copei* has a P^4 that approaches the shape of P^4 of *Leptotomus* (Wood, 1962). This is also true of P^4 of *P. excavatus* which is very similar to that of *P. copei.* Bridgerian *Leptotomus* could easily have been derived from either *P. copei* or *P. excavatus.*

The only change in the dentition of *P. nini* needed to produce the morphology of *P. delicatus* is the full fusion of the hypocone with the protocone on P^4 which has been nearly completed in *P. nini,* and an increase in the rugosity of the enamel on the cheek teeth, which is probably foreshadowed in *P. nini* by the multiple mesostyles on the upper molars.

Thisbemys Wood, 1959*a*

Type species.—*Thisbemys corrugatus* Wood, 1959*a.*

Thisbemys perditus Wood, 1962
(Table 2)

Paramys excavatus gardneri Wood, 1962.
Leptotomus huerfanensis Wood, 1962.
Thisbemys nini Wood, 1962 (in part).
Paramys near *P. excavatus* West, 1973.

Type specimen.—FMNH P 26897, right mandible with M$_2$–M$_3$.

Horizon and locality.—Type from "southwest of Nipple Hollow, about eight miles southwest of Rifle, Colorado" (Wood, 1962:106), Lost Cabin level, Debeque Formation, Colorado. Referred specimens also from Lost Cabin level, Debeque Formation and

Table 2.—*Dental measurements of* Thisbemys perditus. *(compiled from Wood, 1962, Tables 19, 20, 27, 37, 38, 39, 40.) Measurements in millimeters.*

Measurements		N	M	OR
P_4–M_3		9	13.57	12.7–14.65
	a–p	17	3.14	2.84–3.45
P_4	tra	13	2.48	2.27–2.50
	trp	15	2.88	2.55–3.14
M_1	a–p	25	3.04	2.81–3.30
	tra	23	2.75	2.52–3.35
	trp	23	3.02	2.84–3.28
M_2	a–p	24	3.19	2.80–3.42
	tra	19	3.15	2.90–3.51
	trp	21	3.20	2.97–3.60
M_3	a–p	19	3.70	3.10–4.05
	tra	16	3.05	2.78–3.31
	trp	18	2.97	2.63–3.32
I_1	a–p	19	3.75	3.17–4.65
	tra	25	2.37	2.78–3.05
P^4	a–p	2	2.71	2.70–2.72
	tra	2	3.37	3.30–3.43
	trp	2	3.38	3.30–3.45
M^1	a–p	5	3.05	2.84–3.24
	tra	5	3.68	3.53–3.90
	trp	5	3.47	3.33–3.55
M^2	a–p	3	3.18	3.00–3.29
	tra	3	3.63	3.58–3.67
	trp	3	3.32	3.18–3.42
M^3	a–p	2	3.41	3.20–3.63
	tra	2	3.36	3.20–3.52
	trp	2	3.34	3.06–3.61

Upper and Lower Huerfano Formation, Colorado; Cathedral Bluffs Tongue, Wasatch Formation, Wyoming; and possibly the Bridger Formation, Wyoming.

Age.—Late early Eocene to possibly early middle Eocene (Lostcabinian-Gardnerbuttean, and possibly early Bridgerian).

Referred specimens.—FMNH PM 1214-PM 1219 (from Lost Cabin equivalent, Debeque Formation).

AMNH 17545 (from Lower Huerfano Formation, locality VI).

AMNH 17024, 17026, 17451, 17454, 17458, 17459, 17023, 55120, 55121, 55129, 55130, 55132, 55133, 55135, 55137–55139, 55141, 55143, 55146, 55150, 55193, 55196, 55197, 55199, 56542, and USNM 20136 (from the Upper Huerfano Formation).

UW 1363, 1367, 1370, and FMNH PM 15888, PM 15898, PM 21201, PM 21205–PM 21207, PM 21219, PM 21222 (from the Cathedral Bluffs Tongue, Wasatch Formation) and possibly FMNH PM 21076 (from Bridger Formation).

Discussion.—The size and morphology of the cheek teeth of *Thisbemys perditus* are the same as in *Leptotomus huerfanensis* and all specimens referred by Wood (1962) to *T. nini* except the holotype. There is no character that can be used to separate these species. Wood (1962: Fig. 30i) figured the cross-section of a lower incisor of *L. huerfanensis* that was similar to the incisor of other species of *Leptotomus*. However, the specimen figured by Wood, AMNH 55149, is from a mandible with I_1 and M_2 only. The molar in AMNH 55149 is identical to that of *Paramys copei* and should not be referred to the same species as the holotype of *L. huerfanensis*. The incisor in the holotype of *L. huerfanensis*, AMNH 55135, is only partially preserved but it is flattened anteriorly with enamel extending about half the dorsoventral height of the tooth on the lateral side. The widest part of the tooth is near its center. This tooth is the same as those figured by Wood (1962: Figs. 18q, 18r, and 37h, 37o) for *P. excavatus gardneri*, *T. perditus* and *T. nini*. The shallow groove on I_1 of *T. perditus* is variably present as in species of *Paramys*.

A previously undescribed maxilla with P^4–M^2 from the Upper Huerfano, AMNH 56542, has been identified in the AMNH collections as *Leptotomus huerfanensis*. This specimen shows irregularities in the enamel of the cheek teeth, P^4 without a hypocone, origin of the anterior root of the zygoma the same as in other paramyines, equivalent size to *T. perditus*, and is virtually identical to upper dentitions previously referred to *P. excavatus gardneri* and *T. perditus*. This specimen in no way resembles any species of *Leptotomus* except in features common to all paramyines. AMNH 56542 should be referred to *T. perditus*.

Specimens from the Cathedral Bluffs Tongue of the Wasatch Formation referred by West (1973) to *Paramys* near *P. excavatus* appear to be referable to *T. perditus*. Wood (1962) previously had cited a few specimens of *T. perditus* from the Cathedral Bluffs in the original hypodigm of the species. One specimen, P^4, from the Bridger Formation (FMNH PM 21076) was referred by West (1973) to *Paramys* near *P. excavatus* along with the specimens from Cathedral Bluffs. He noted that this specimen was identical to P^4 of *P. copei* or *P. excavatus* but was closer in size to the latter. Earlier, Wood (1959*a*) identified two isolated lower molars from Tabernacle Butte (Upper Bridger Formation) as *Paramys* cf. *excavatus*. These three specimens may represent a small Bridgerian species of *Paramys*, but the material is too poor to determine this at present.

Guthrie (1971) referred all of the specimens from

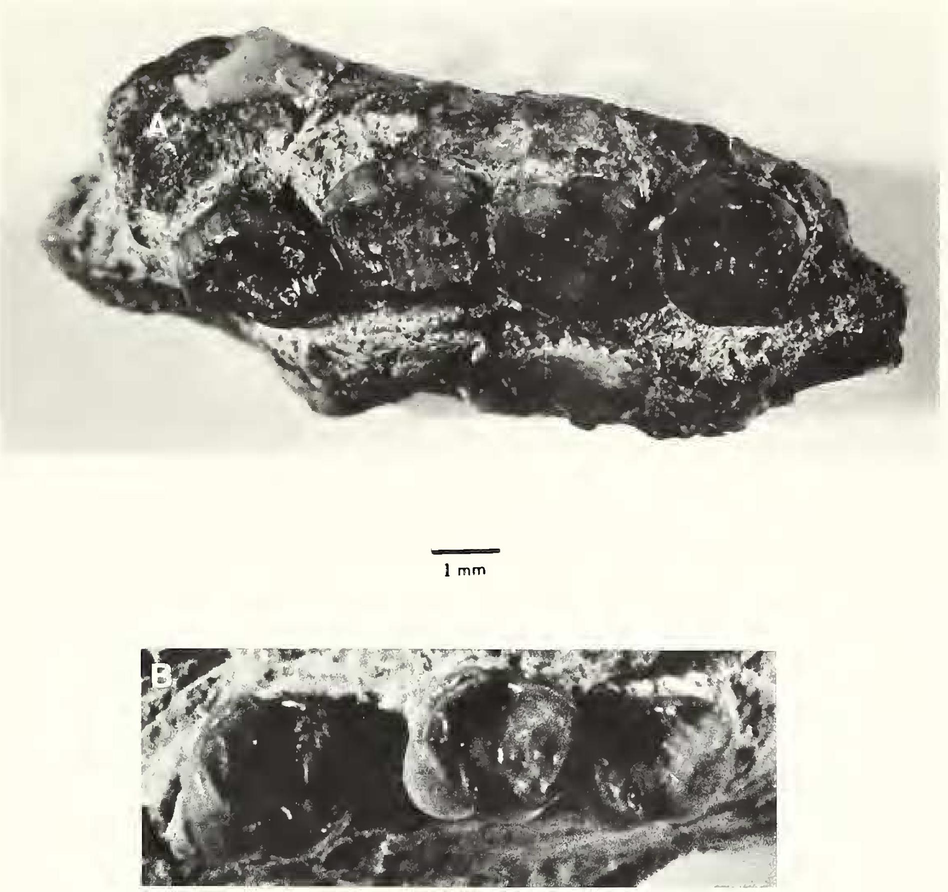


Fig. 5.—Dentition of *Thisbemys elachistos*. A) LP^4–M^3, AMNH 55122. B) RP$_4$–M$_2$, CU 23459 (type).

the Lost Cabin Member of the Wind River Formation identified by Wood (1962) as *T. perditus* to *Paramys copei*. There are no specimens in the extensive collections from the Wind River Basin at Carnegie Museum of Natural History that can be referred to *T. perditus*. The specimens figured by Wood from the Wind River Basin appear to be referable to either *P. excavatus* or *P. copei* in size and morphology (see Guthrie, 1971). None of the specimens referred to *T. nini* by Wood (1962) from the Upper Huerfano can be separated from *T. perditus*. The occurrence of *T. perditus* is thus limited to the Lost Cabin equivalent of the Debeque Formation, Huerfano Formation, Cathedral Bluffs Tongue, and possibly the Bridger Formation. Wood's (1962) identification of three different species of three genera from the Upper Huerfano, *Paramys excavatus gardneri*, *Leptotomus huerfanensis*, and *Thisbemys nini*, seems untenable and a single species, *Thisbemys perditus*, is here recognized in that unit.

Thisbemys elachistos, new species
(Fig. 5, Table 3)

Type specimen.—CU 23495, associated mandibles with LM$_1$–M$_2$ and RP$_4$–M$_2$.

Horizon and locality.—Locality II (see Robinson, 1966), Upper Huerfano Formation, Colorado.

Age.—Latest early Eocene (Gardnerbuttean).

Referred specimens.—CU 32161, RM$_1$–M$_3$; AMNH 55122, LP^4–M^3.

Diagnosis.—Smallest species of the genus; accessory lophs on cheek teeth broad and persistent until teeth heavily worn; P^4 nearly square in occlusal outline; M^3 also square with minute hypocone; masseteric fossa ends below anterior end of M$_2$.

Etymology.—*elachistos*, Greek, smallest.

Description.—P^4 is roughly square in occlusal outline. The protoloph is shorter than the metaloph. Both anterior and posterior cingula extend the entire width of the tooth. The metaconule is

Table 3.—*Dental measurements of* Thisbemys elachistos *and* Thisbemys *sp. Measurements in millimeters.*

Specimen no.	P_4			M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
					Thisbemys sp.							
PU 18418	—	—	—	—	—	3.46	3.63	3.46	—	4.13	3.46	—
					Thisbemys elachistos							
CU 23495 L	—	—	—	2.30	2.02	2.16	2.25	2.15	2.24	—	—	—
CU 23495 R	2.12	1.76	1.85	2.25	2.06	2.11	2.31	2.21	2.21	—	—	—
CU 32161 L	—	—	—	2.12	—	1.98	2.18	2.08	2.16	2.39	1.93	2.
CU 32161 R	—	—	—	2.12	1.83	2.02	2.17	2.12	2.15	2.29	1.95	1.
		P^4			M^1			M^2			M^3	
AMNH 55122	1.95	2.22	2.36	2.15	2.40	2.30	2.14	2.32	2.13	2.00	2.17	

large, nearly equal in size to the metacone. Accessory lophs running into the central basin of the tooth are short and broad. On the posterolingual corner of the tooth is a nearly circular wear facet. Anterior to it is a very narrow and shallow valley that separates it from a second nearly circular facet at the center of the lingual margin. Anterior to this second swelling at the anterolingual corner of the tooth is the protocone which is a larger wear facet with dentine exposed at its center. Neither of the two "cusps" posterior to the protocone appear to be homologous to the hypocone but are merely irregularities in the posterior cingulum.

M^1 and M^2 are nearly identical, and agree in general shape with those in other species of *Thisbemys*. The accessory lophs are short and broad as in P^4. M^3 is very close to M^2 in shape. The metacone is reduced to a small cuspule on the posterobuccal corner of the tooth, and the hypocone is just a minor swelling on the posterior cingulum. There is no posterior elongation or reduction of the hypocone area of this tooth.

I^1 is convex anteriorly with enamel extending half way up the lateral side of the tooth, and just slightly onto the medial side.

The masseteric fossa on the mandible extends anteriorly to below the posterior margin of M_1. There are two mental foramina on the mandible. A larger mental foramen is situated fairly low on the mandible, near mid-depth, and just anterior to P_4. A second, smaller foramen is lower on the mandible and beneath the posterior root of P_4.

P_4 is molariform but smaller than M_1. The metaconid is the largest cusp on the tooth. The trigonid basin is minute but present. The posterolophid is a broad continuous loph that runs from the hypoconid to the entoconid. Accessory lophs on P_4 are reduced to irregular swellings in the talonid basin.

The lower molars are rectangular in occlusal shape, increase in size posteriorly and do not differ markedly from those of *Thisbemys perditus*. The accessory lophs are short and broad but persist until the teeth are heavily worn. The lower incisor is parallel sided and flattened anteriorly on the holotype, and slightly concave anteriorly on the referred specimen. Enamel on the medial and lateral sides of the lower incisor is the same as for I^1.

Discussion.—*Thisbemys elachistos* is smaller than any other species of the genus. The nature of the accessory crenulations of the cheek teeth is similar to that of *T. perditus* in being low and relatively broad. P^4 of *T. elachistos* differs from that of all other species of *Thisbemys* in being more nearly square in occlusal outline.

Thisbemys elachistos and *T. perditus* are probably closely related and differ from all other *Thisbemys* in the number and nature of the accessory lophs or crenulations on the cheek teeth. All other species of *Thisbemys* have a network of fine crenulations on the cheek teeth. The condition in *T. elachistos* and *T. perditus* does not appear primitive for *Thisbemys*, but separately derived. The presence of an older species (described below but not named) that has irregularities of the enamel that approach the condition in other *Thisbemys* helps to support this suggestion.

***Thisbemys* sp.**

(Fig. 6, Table 3)

Referred specimen.—PU 18418, right mandible with M_2–M_3 and talonid of M_1.

Horizon and locality.—Type area of the Lysite Member, Wind River Formation, Wyoming.

Age.—Middle early Eocene (Lysitean).

Description.—PU 18418 is equal in size to the Bridgerian *Thisbemys plicatus* and *T. corrugatus*. The masseteric fossa ends anteriorly below the posterior margin of M_2. The lower incisor is flattened medially and rounded anteriorly and laterally. Enamel extends only slightly onto the medial face of the incisor and about half way up the lateral face.

The occlusal pattern of M_2 and M_3 of PU 18418 does not differ from the basic paramyine pattern. Within the talonid basins of the molars are numerous small irregularities of the enamel. These irregularities are relatively small and low, possibly disappearing with heavier wear. The posterolophid is broken by a series of small narrow valleys, probably part of the system of irregularities of the enamel. These irregularities are isolated from one another and are not connected into elongate lophs or crenulations.

Discussion.—PU 18418 more closely resembles

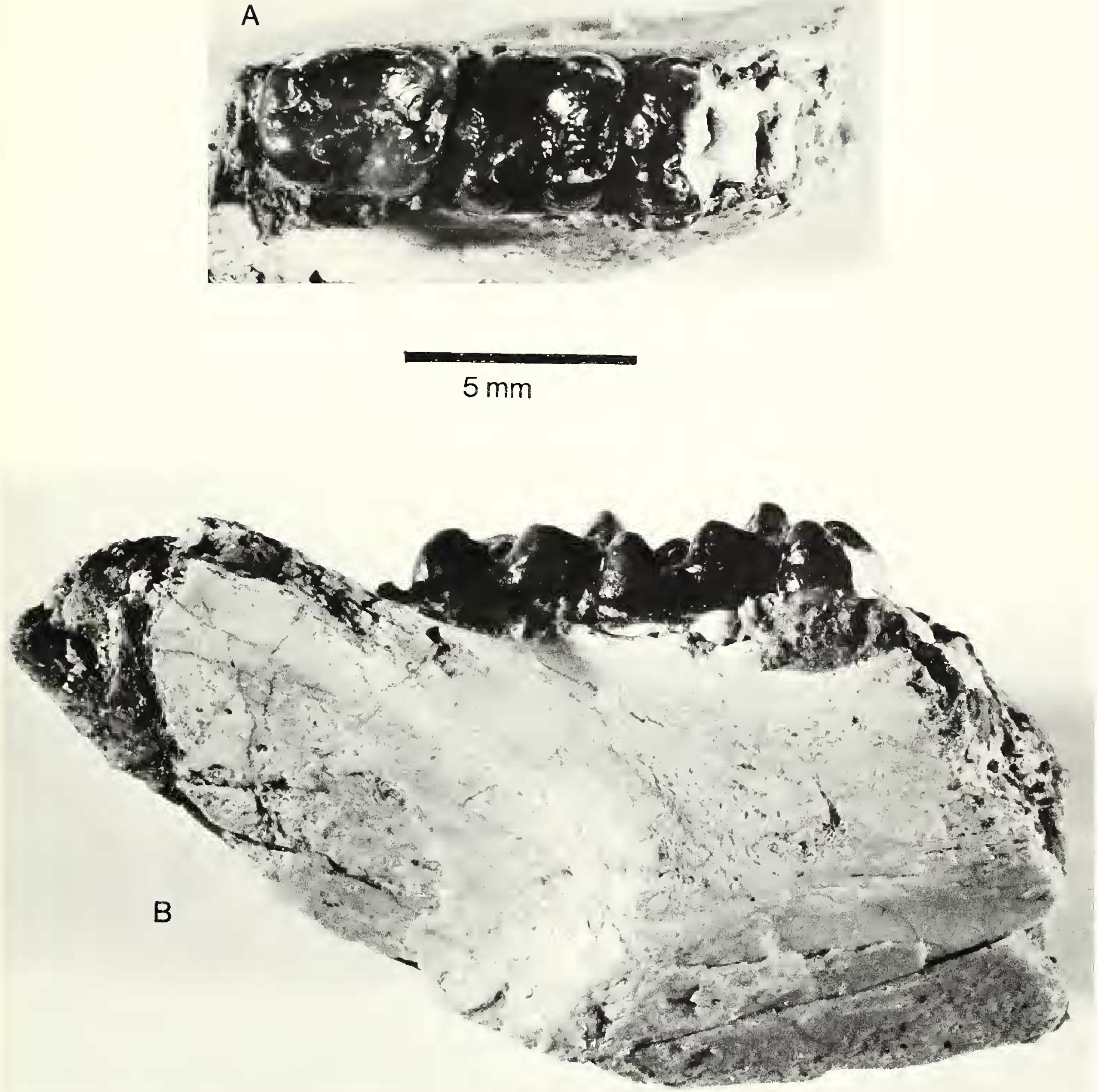


Fig. 6.—*Thisbemys* sp., M_1 (part)–M_3, PU 18418. A) Occlusal view. B) Lateral view of mandible.

the Bridgerian species *Thisbemys plicatus* and *T. corrugatus* than any other rodent. PU 18418 differs from these species in having less prominent irregularities of enamel in the basins of the lower molars that are not connected into minute crests.

There is nothing in the morphology of PU 18418 that would remove it from being a possible ancestor of *T. plicatus* or the later species of *Thisbemys*. The remaining early Eocene species of this genus, *T. perditus* and *T. elachistos*, represent a separate lineage from that represented by PU 18418 and the middle and late Eocene species of *Thisbemys*. Wood (1962) noted this same natural separation of *T. perditus* (and "*T. nini*") from the other species.

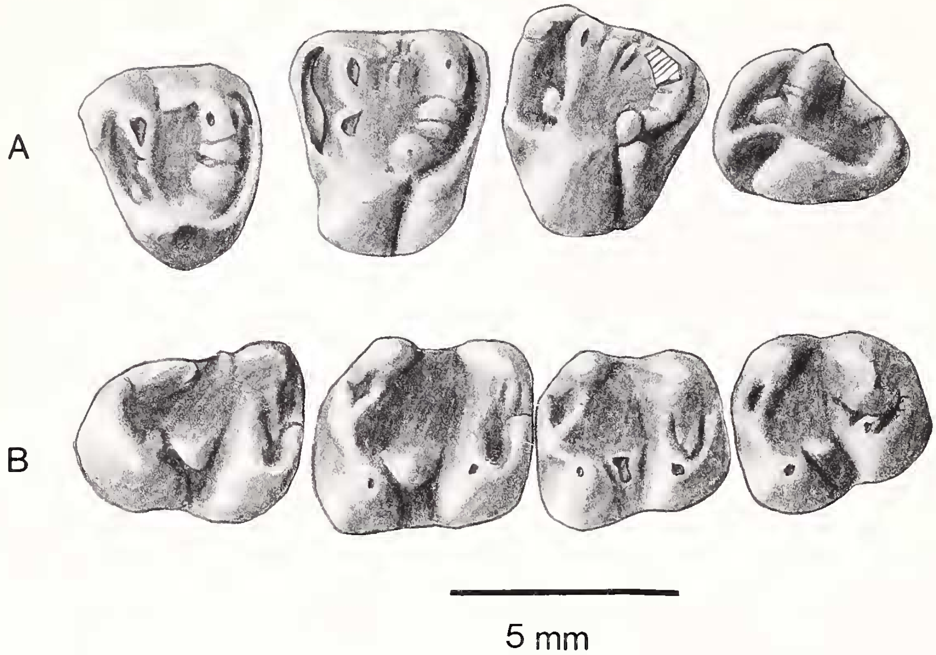


Fig. 7.—Cheek teeth of *Notoparamys costilloi.* A) LP^4–M^3, AMNH 55111 (type). B) RP$_4$–M$_3$, AMNH 55113.

Leptotomus Matthew, 1910

Type species.—Leptotomus leptodus (Cope, 1873).

Leptotomus cf. ***L. bridgerensis*** Wood, 1962

Referred specimen.—AMNH 55951, isolated LP^4 and LM^3.

Horizon and locality.—Locality III, Upper Huerfano Formation, Colorado.

Age.—Latest early Eocene (Gardnerbuttean).

Discussion.—Wood (1962) assigned two isolated teeth, P^4 and M^3 (AMNH 55951), from the upper Huerfano to *Leptotomus* cf. *L. parvus.* He recognized that the P^4 was distinct from that of *L. parvus,* but was of similar size.

AMNH 55951 is also very close to *L. bridgerensis* in size. The features of P^4 which distinguish AMNH 55951 from *L. parvus* (markedly tapered lingually, large mesostyle) are features of P^4 of *L. bridgerensis.* The P^4 of *L. parvus* is virtually inseparable from those of Bridgerian *Paramys,* as are the molars, suggesting that this species may well be referable to *Paramys* rather than *Leptotomus.*

Notoparamys, new genus

Type species.—Notoparamys costilloi (Wood, 1962).

Range.—Early Eocene of Colorado, New Mexico and possibly Wyoming.

Referred species.—Notoparamys arctios, new species.

Diagnosis.—P^4 submolariform but lacking hypocone; hypocone on M^1–M^2 distinct and buccally positioned adjacent to metaconule; M^3 small relative to M^1–M^2; mesoconid large on lower molars; hypoconulid on P$_4$–M$_2$ large, elongate transversely, lingually placed and connected to entoconid by two minute ridges originating from the lingual end of the hypoconulid; an accessory lophid runs buccally into the trigonid basin from the metaconid on the molars; I$_1$ is flattened medially and rounded laterally.

Etymology.—notos, Greek, southern; and *Paramys,* a closely related Eocene rodent.

Comparisons.—Notoparamys differs from other paramyines by the unique double attachment of the hypoconulid to the entoconid on the lower cheek teeth, cross-sectional shape of I$_1$, the deep groove separating the hypocone from the protocone on M^1–M^2, more buccal position of the hypocone on the upper molars, and larger mesoconid on the lower cheek teeth. *Notoparamys* also differs from *Thisbemys* in the fine crenulations present in the basins of the cheek teeth of the latter are not found on the former.

Notoparamys differs from *Rapamys* by the lack of enlarged metaconules on the upper cheek teeth, and from *Uriscus* by the occlusal outline of the lower molars. *Notoparamys* differs from all other ischyromyids by the characters listed above under the diagnosis of the Paramyini.

Notoparamys costilloi (Wood, 1962)
(Fig. 7)

Type specimen.—AMNH 55111, crushed skull with left and right P^4–M^3.

Horizon and locality.—Type and some referred specimens from locality VIII, Lower Huerfano Formation, Colorado. Other specimens from Almagre Member, San Jose Formation, New Mexico.

Age.—Late and possibly middle early Eocene (Lostcabinian and possibly Lysitean).

Referred specimens.—AMNH 55110, crushed skull; AMNH 55113, two complete mandibles (from Lower Huerfano); AMNH 80686, M^2; AMNH 80727a, I$_1$ (from Almagre Member, San Jose Formation).

Emended diagnosis.—Intermediate sized paramyine (see Wood, 1962: Tables 27, 28); metaconules doubled on P^4–M^2; low broad accessory lophs originate from the metaconid and protoconid and run into the trigonid basins of M$_1$–M$_3$; double lophs connecting the entoconid and hypoconulid relatively high, posterior loph broken at its center by narrow valley.

Discussion.—Wood (1962) first described *Leptotomus costilloi,* basing the generic reference on the cross-sectional shape of the lower incisor. Guthrie (1967) noted several differences in the dentition of *L. costilloi* from other species of *Leptotomus* but followed Wood's allocation because of the shape of the lower incisor. However, the I$_1$ of "*L.*" *costilloi* is quite distinct from that of species of *Leptotomus* such as *L. leptodus* and *L. bridgerensis* in being much broader, nearly circular in cross-section, enamel not extending as far posteriorly on the lateral surface, not having a narrow (nearly pointed) anterior face, and having its widest point near the center of the tooth.

The molars are equally distinct from those of *Leptotomus.* In the lower molars, the connection of the posterolophid to the entoconid, large isolated mesoconids, unique connection of the hypoconulid to the entoconid and larger trigonid basins filled with accessory lophids are not present in any species of *Leptotomus.* The upper cheek teeth of *Notoparamys costilloi* are also distinct from those of *Leptotomus* in the shape of the teeth and size and position of the hypocone on M^1–M^2. *Notoparamys costilloi* is not congeneric with *Leptotomus* and is unique among paramyines.

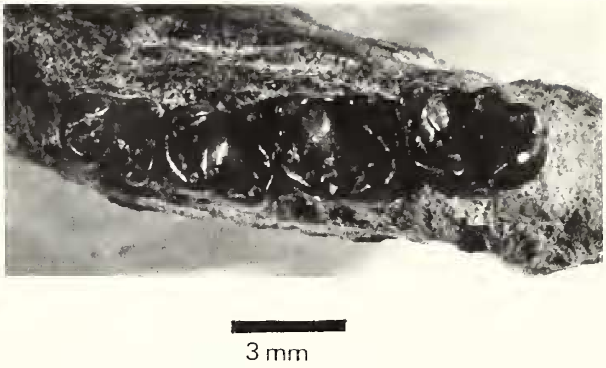


Fig. 8.—Holotype of *Notoparamys arctios,* FMNH P 26503, LP$_4$–M$_3$.

An isolated lower molar (AMNH 80686) and an I$_1$ (AMNH 89727a) from the Almagre Member of the San Jose Formation, New Mexico, closely resemble those of *N. costilloi.* the isolated M$_2$ is slightly smaller than the specimens from the Huerfano (Table 5). There are no accessory lophids filling the trigonid basin, and the minute valley between the double lophids that connect the entoconid and hypoconulid is less anteroposteriorly compressed. The lower incisor is identical to I$_1$ of *N. costilloi* from the Huerfano but is also slightly smaller (Table 5). These two specimens are referred to *Notoparamys* cf. *N. costilloi.*

A single M^1 (AMNH 4222g) from an unknown level in the Willwood Formation, Wyoming, also shows some similarities to *N. costilloi.* AMNH 4222g is slightly smaller than M^1 of *N. costilloi* from Colorado. The metaconule is buccolingually elongate but not multiple as in the Colorado material. All other features of AMNH 4222g agree with *N. costilloi.* This specimen is too large to be referred to the Lysitean species of *Notoparamys* (described below) and differs enough from *N. costilloi* that it may represent a new species. AMNH 4222g is here identified as *Notoparamys* sp.

Notoparamys arctios, new species
(Fig. 8, Table 4)

Reithroparamys debequensis Wood, 1962 (in part).

Type specimen.—FMNH P 26503, left mandible with P$_4$–M$_3$.

Horizon and locality.—Charard Park, "about five

Table 4.—*Dental measurements of* Notoparamys *(in millimeters).*

Measurements		*Notoparamys arctios* (FMNH P 26503)	*Notoparamys* cf. *N. costilloi* (AMNH 80686)	*Notoparamys* sp. (AMNH 4222g)
P_4–M_3		12.89		
P_4	a–p	2.67		
	tra	2.02		
	trp	2.32		
M_1	a–p	3.02	3.84	
	tra	2.49	3.36	
	trp	2.76	3.62	
M_2	a–p	3.09		
	tra	2.84		
	trp	2.93		
M_3	a–p	3.96		
	tra	2.91		
	trp	2.59		
M^1	a–p			3.61
	tra			4.48
	trp			4.11
			(AMNH 80727)	
I_1	a–p		3.16	
	tra		2.16	

miles southwest of Rifle, Colorado" (Wood, 1962: 134), Lysite equivalent, Debeque Formation.

Age.—Middle early Eocene (Lysitean).

Hypodigm.—Type only.

Diagnosis.—Small species; no accessory ridge in the trigonid basin from the protoconid; parallel ridges connecting entoconid and hypoconulid minute and the posterior one not broken by narrow valley; I_1 more nearly parallel sided.

Etymology.—*arctios*, Greek, northern.

Description.—The mandible and lower teeth of *Notoparamys arctios* are quite similar to those of *N. costilloi* but are about one-third smaller. The cheek teeth of *N. arctios* have smaller mesoconids and hypoconulids, less bulbous cusps and weaker connections of the entoconid to the hypoconulid on the lower cheek teeth than in *N. costilloi.*

Both M_1 and M_2 of *N. arctios* have a low, broad loph running from the metaconid into the trigonid basin. This feature is much more pronounced in *N. costilloi.* Because the small lophs connecting the hypoconulid to the entoconid are much smaller on the molars of *N. arctios*, the small depression surrounded by these lophs is much shallower.

The trigonid of M_3 is relatively larger than in *N. costilloi* and lacks any accessory lophs within it. The hypoconulid on M_3 of *N. arctios* is separated from the entoconid by a distinct valley and forms a separate posterolingual lobe on the tooth.

The lower incisor is relatively broad, convex anteriorly and laterally, and flattened medially. The widest part of the incisor is at one-third the dorsoventral height of the tooth. Enamel extends laterally about half the dorsoventral height of the tooth, and just slightly onto the medial surface.

Discussion.—*Notoparamys arctios* differs from *N. costilloi* in its smaller size, less prominent cusps, weaker connection of the entoconid and hypoconulid, fewer accessory lophs in the trigonids of the molars, and shape of the lower incisor. In all these features *N. arctios* is more primitive than *N. costilloi.* There are no features of *N. arctios* that would remove it from an ancestral position to *N. costilloi. Notoparamys arctios* is also known from older levels (Lysitean) than *N. costilloi* (Lostcabinian).

The holotype of *N. arctios* cannot be referred to *Reithroparamys debequensis* as was originally done by Wood (1962). *Notoparamys arctios* is larger and the molars are relatively broader than *R. debequensis. Notoparamys arctios* also lacks the separation of the entoconid from the posterolophid on the molars and the associated partial hypolophid that are present in *R. debequensis.*

Tribe Manitshini Simpson, 1941*b*

Included genera.—*Manitsha* Simpson (1941*a*), *Pseudotomus* Cope (1872), *Ischyrotomus* Matthew (1910), and *Quadratomus*, new genus.

Discussion.—Simpson (1941*b*) originally included only the North American genera *Manitsha, Psueodtomus* and *Ischyrotomus* in the Manitshini. Wood (1962) raised the rank of the group to subfamily and included the European genus *Plesiarctomys.* Michaux (1968) included *Plesiarctomys* in the Pseudoparamyinae based predominantly on the lack of P^3. Wood (1970), in his review of the genus, included *Plesiarctomys* in the Manitshinae and pointed out that at least a dP^3 is present in most specimens of *Plesiarctomys* but later (Wood, 1976*a*) followed Michaux in including *Plesiarctomys* in the Pseudoparamyinae.

Even if *Plesiarctomys* possesses a P^3, all of its features shared with manitshines are allometric changes. All other features of *Plesiarctomys* agree with Michaux's (1964, 1968) definition of the Pseudoparamyinae.

The inclusion of *Quadratomus* does not alter Simpson's (1941*b*:142) diagnosis for the tribe except for the shape of the lower incisor and possession of a heavy chin process or "symphyseal flange" on the mandible.

Quadratomus, new genus

Type species.—*Quadratomus grandis* (Wood, 1962).

Range.—Late early Eocene of Colorado, middle Eocene of Wyoming, and possibly early Oligocene of Texas.

Referred species.—*Quadratomus* sp. and ?*Q. gigans* (Wood, 1974).

Diagnosis.—Anterior root of the zygoma arises buccal to M^1 and arches dorsally; masseteric fossa ends between M_2–M_3 on the mandible; lower incisor narrow anteriorly with small flat surface, greatest width posterior; upper molars nearly square in occlusal outline; lophs on the molars very low and broad, separated by a shallow broad central basin; hypocone small on upper molars; trigonid basins on lower molars anteroposteriorly compressed, closed anteriorly and nearly closed posteriorly by narrow ridges from the metaconid and protoconid; talonid basins broad and shallow; mesoconid minute; ectolophid absent; anterior and posterior transverse widths of the lower molars nearly equal; M_3 elongate; lower molars longer than wide; posterolophid continuous with entoconid on lower cheek teeth; no heavy chin process on the mandible.

Etymology.—*quadratos,* Latin, squared; *mus,* Latin, mouse.

Comparisons.—Though the morphology of the cheek teeth, general size and massiveness of the mandible, and modification of the ventral margin of the zygoma of *Quadratomus* make it referable to the Manitshini, it differs from all other manitshine genera in the shape of the lower incisor, lack of a heavy chin process on the mandible, position of the anterior root of the zygoma, and in having lower molars longer than wide.

Quadratomus grandis (Wood, 1962)
(Fig. 9)

Leptotomus grandis Wood, 1962

Type specimen.—USNM 10137, mandible with P_4–M_3, postcranial and skull fragments and I^1.

Horizon and locality.—Type and referred specimens from localities II and III, Upper Huerfano Formation, Colorado.

Age.—Latest early Eocene (Gardnerbuttean).

Referred specimens.—AMNH 17452, 17453, 17457, 55126, 55192.

Emended diagnosis.—Average size for a manitshine (see Wood, 1962: Tables 27, 28); minute irregularities on cheek teeth; I_1 may have anterior sulcus; mesoconids present on lower molars; posterior margin of anterior root of zygoma level with the paracone of M^1.

Discussion.—Wood (1962) thoroughly described *Leptotomus grandis.* No additional material has been found since that time so no further description is necessary.

Wood (1962) referred this species to the *Leptotomus,* as he did with *Notoparamys costilloi,* on the basis of the shape of the lower incisor, even though he noted the considerable difference between I_1 of *L. grandis* and other species of *Leptotomus.* I_1 of *Quadratomus grandis* is clearly distinct from that of *Leptotomus.* It is flattened and much broader anteriorly, not tapering anteriorly as markedly. The lower incisors of *Q. grandis* most closely resemble those of *Paramys delicatus,* except they are slightly narrower. The lower cheek teeth of *Q. grandis* are more similar to those of manitshines and differ from those of *Leptotomus* in having: 1) lower molars not lophate; 2) cusps more marginal and less distinct; 3) posterolophid connected to the entoconid; 4) trigonid basins more anteroposteriorly compressed; 5) enamel not smooth on cheek teeth; and 6) talonid basins large and shallow. The upper teeth differ from those of *Leptotomus* in having: 1) nearly square occlusal outline; 2) P^4 relatively longer; 3) protoloph and metaloph broadly separated, leaving shallow, broad trigon basin; and 4) less cingular development on the parastylar area. The maxilla of *Q. grandis* also differs from that of *Leptotomus* in the more posterior placement of the anterior root of the zygoma and the nearly vertical broad anterior face of the zygoma. The unusual ventral part of the anterior root of the zygoma noted by both Wood (1962) and Black (1971) arches dorsally. This arrangement of the zygoma is known elsewhere only in manitshines.

West (1973) referred a partial skeleton with all upper and lower teeth from the Bridger Formation to *Pseudotomus robustus.* This specimen, however, is clearly congeneric with *Q. grandis* and distinct from *Pseudotomus* and other manitshines in: 1) lower crowned cheek teeth; 2) trigonids on lower molars broader; 3) lower molars longer than wide; 4) I_1 narrow; 5) mandible more slender without heavy chin process; 6) upper molars much longer; and 7) anterior root of the zygoma more posteriorly positioned. The Bridgerian material represents a distinct species of *Quadratomus* that will be described elsewhere. The two specimens of *L. grandis* cited by Wood (1962) from the Bridger Formation are probably not referable to *Q. grandis,* and are within the size range of *L. bridgerensis.*

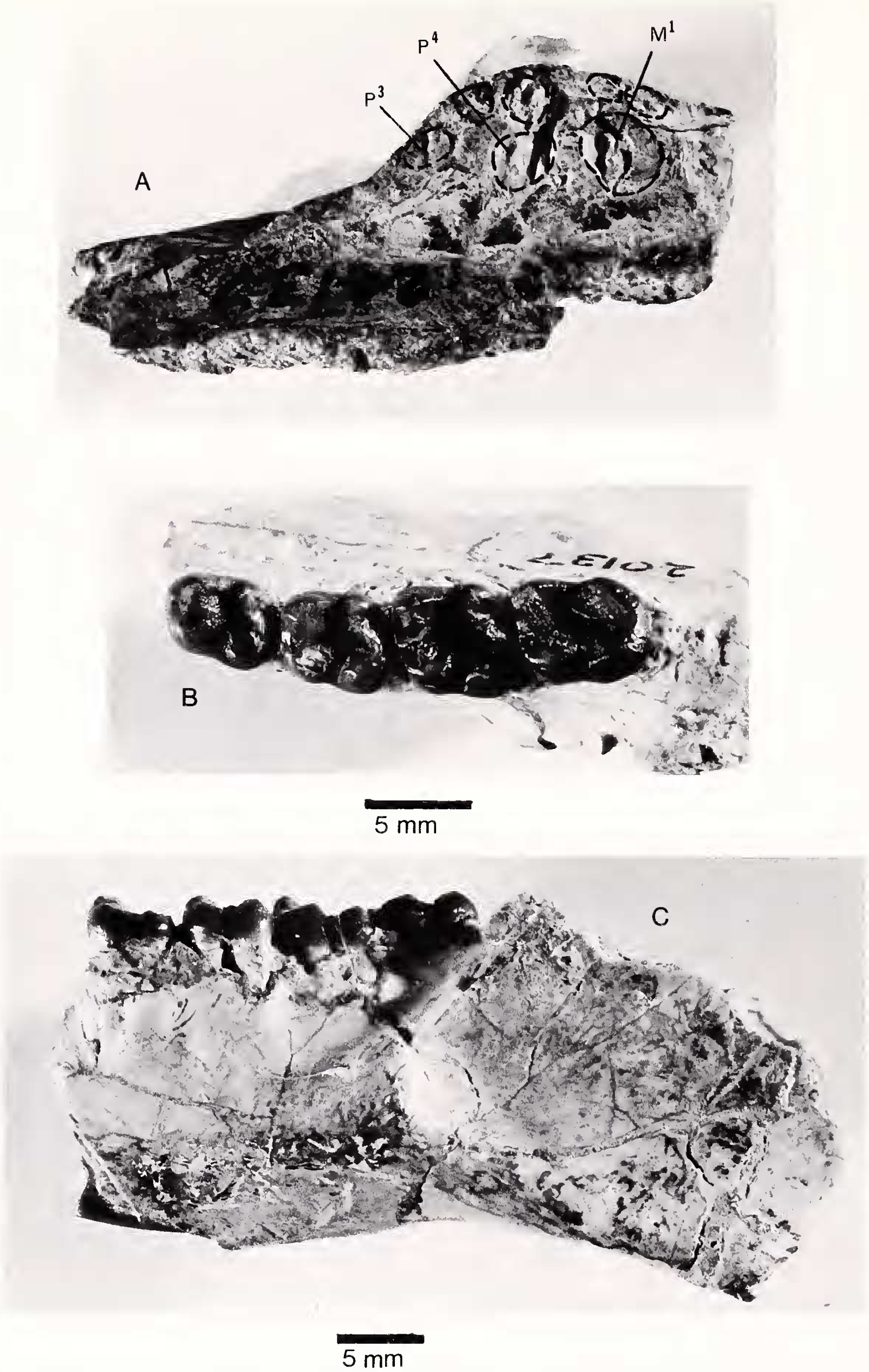


Fig. 9.—Holotype of *Quadratomus grandis,* USNM 20137. A) Ventral view of maxilla with alveoli for P^3–M^1. B) Occlusal view of LP$_4$–M$_3$. C) Lateral view of mandible.

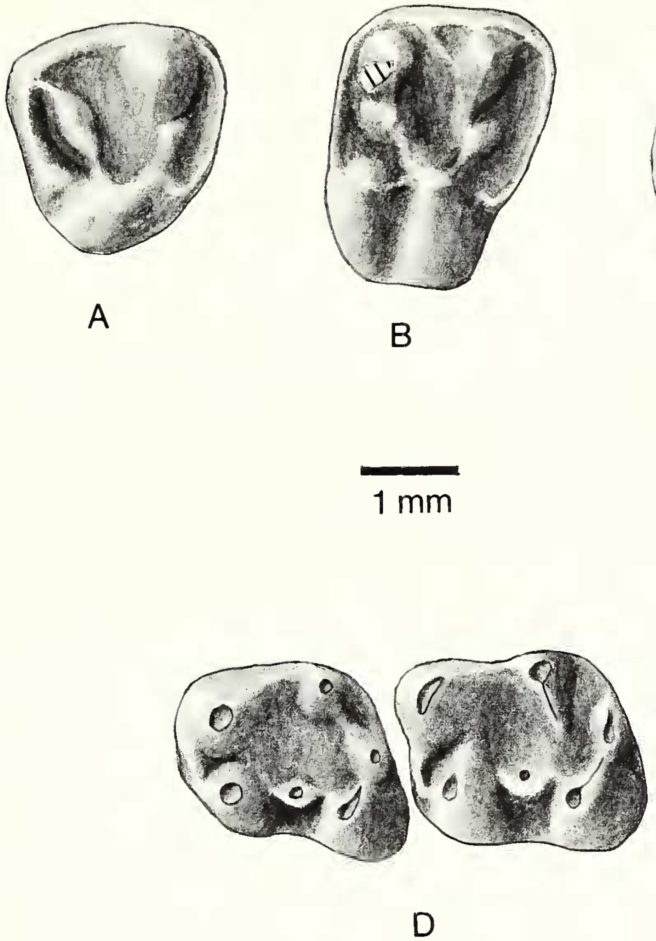


Fig. 10.—Cheek teeth of *Reithroparamys ctenodactylops.* A) RM^3, UW 15010. B) RM^1 or M^2, UW 15263. C) RP^4, UW 15262. D) LM$_1$–M$_2$, UW 15008 (holotype).

Wood (1974) described a large species, *Leptotomus gigans,* from the early Oligocene Vieja Group, Texas. This species, however, has a lower incisor that more nearly approaches that of *Quadratomus,* and molars that more closely resemble typical manitshines. The mandible of *L. gigans* is more slender than manitshines, and more similar to that of *Quadratomus.* The lower cheek teeth are low crowned, massive, and nearly square in occlusal outline as in *Quadratomus.* The occlusal pattern of the teeth of *L. gigans* differs from that of manitshines and *Quadratomus* in having a trigonid that is not as anteroposteriorly compressed. The partial hypolophid on the lower cheek teeth of *L. gigans* is not present in *Q. grandis* or the Bridgerian species of *Quadratomus* but a complete hypolophid is present in *Manitsha tanka.*

Overall, *Leptotomus gigans* more closely resembles *Quadratomus* than any other genus of ischyromyid, but cannot be definitely referred to this genus. Therefore, *L. gigans* is here questionably referred to *Quadratomus* as ?*Q. gigans.*

Simpson (1941*b*) viewed the members of the Manitshini as representing a single lineage leading to the Oligocene genus *Manitsha. Quadratomus* represents a separate lineage ending in the early Oligocene with ?*Q. gigans.*

Subfamily Reithroparamyinae Wood, 1962

Emended diagnosis.—Small to medium sized ischyromyids; auditory bulla large and coosified with the skull; posterior margin of nasal bones level with that of premaxillaries; posterior margin of anterior root of zygoma level with center of P^4 or farther anterior; incisors narrow; mandible slender; P^4 molariform with hypocone present; M^1 nearly equal in size and proportions to M^2; hypocones on upper molars relatively large; metaconid lingually positioned on M^1–M^2; entoconid separated from posterolophid; hypoconulid present on lower molars.

Included genera.—*Reithroparamys* Matthew (1920), *Microparamys* Wood (1959*a*), *Lophiparamys* Wood (1962), *Acritoparamys*, new genus, and possibly *Apatosciuravus*, new genus.

Comparisons.—The Reithroparamyinae differ from paramyines in having nasal bones extending posteriorly to the same level as the premaxillaries on the dorsal side of the skull, the anterior root of the zygoma and masseteric scar on the mandible anteriorly placed, and being generally smaller in size. They differ from paramyines, pseudoparamyines and manithines in having hypocone on P^4, relatively larger hypocone on M^1–M^2, isolated entoconid and larger hypoconulid on the lower molars, and having a bony auditory bulla attached to the skull. This last feature is only known for *Reithroparamys delicatissimus* and "*Paramys*" *sciuroides* Scott and Osborn (1887; not referable to *Leptotomus* but rather *Reithroparamys*) and may not be true for all reithroparamyines. The Reithroparamyinae differ from the Ischyromyinae by having lower crowned, less lophate teeth; and having a small infraorbital foramen with no associated modification of the zygomasseteric structure.

Discussion.—Originally, Wood (1962) included *Reithroparamys, Rapamys,* and his new genera *Franimys* and *Tapomys* in the Reithroparamyinae. One of the major characters uniting these genera was the possession of an "incipiently hystricognathous" mandible. Wood (1962) repeatedly compared the Reithroparamyinae with the early Oligocene hystricognathous rodent *Platypittamys* from South America. As discussed above, none of the reithroparamyines are hystricognathous or "incipiently hystricognathous," but are entirely sciurognathous and any similarities between them and early South American hystricognathous rodents are superficial.

Black (1971) was the only other author to diagnose the subfamilies of the Ischyromyidae. He referred *Rapamys* to the Paramyinae and included *Microparamys, Lophiparamys,* and the late Eocene *Janimus* in the Reithroparamyinae along with Wood's included genera. Black (1971) synonymized *Tapomys* under *Leptotomus,* which he included in the Paramyinae.

Wood's (1976*a*) later subfamilial arrangement was virtually identical to his first. He did not follow Black's (1971) synonymy of *Tapomys* and included *Janimus* in the Microparamyinae.

The classification followed here more closely follows that of Black (1971). *Franimys,* previously considered a reithroparamyine by both Black (1971) and Wood (1962, 1976*a*), appears more closely related to the European *Pseudoparamys* and is here placed in the Pseudoparamyinae of Michaux (1964). Both Dawson (1966, 1977) and Wood (1974) compared *Janimus* with early Oligocene *Eutypomys* and suggested a possible relationship. *Janimus* is here referred questionably to the Eutopomyidae.

Reithroparamys Matthew, 1920

Type species.—*Reithroparamys delicatissimus* (Leidy, 1871).

Reithroparamys ctenodactylops, new species

Type specimen.—UW 15008, partial left mandible with M_1–M_2.

Horizon and locality.—Type and all referred specimens from SW¼, NW¼, SW¼, sec. 20, T16N, R101W (UW locality V-60008), 1789′ below Luman Tongue, Wasatch Formation, Sweetwater County, Wyoming.

Age.—Early early Eocene (Graybullian).

Referred specimens.—UW 15009, LM^1 or M^2; UW 15010, RM^3; UW 15262, RP^4; UW 15263, RM^1 or M^2.

Diagnosis.—Smallest species of the genus; upper molars relatively short with large conules and hypocone lingual to the protocone; hypoconulid on lower molars large and conical; posterolophid weakly developed on lower molars.

Etymology.—*ctenodactylops, Ctenodactylus*-like, in reference to features shared by this species with early Tertiary ctenodactyloids of Asia.

Description.—M_1 and M_2 of *Reithroparamys ctenodactylops* closely resemble those of other *Reithroparamys* with an entoconid isolated from the posterior cingulum with a partial hypolophid running buccally into the talonid basin. The trigonid of M_1–M_2 are narrower than the talonids with the protoconid and metaconid placed closely together. The trigonid basin is reduced to a narrow valley between the protoconid and metaconid which runs anteroposteriorly. The anterior cingulum on M^1–M^2 is a very short loph running from the buccal margin of the base of the metaconid buccally to the level of the apex of the protoconid. The mesoconid is relatively large and distinct. The hypoconulid is much enlarged, being nearly equal in size to the entoconid and hypoconid. Only a very low posteroloph connects the hypoconulid to the hypoconid. M_1 is smaller than M_2.

P^4 is submolariform and smaller than the upper molars. Both the protoloph and metaloph are fully developed with large dis-

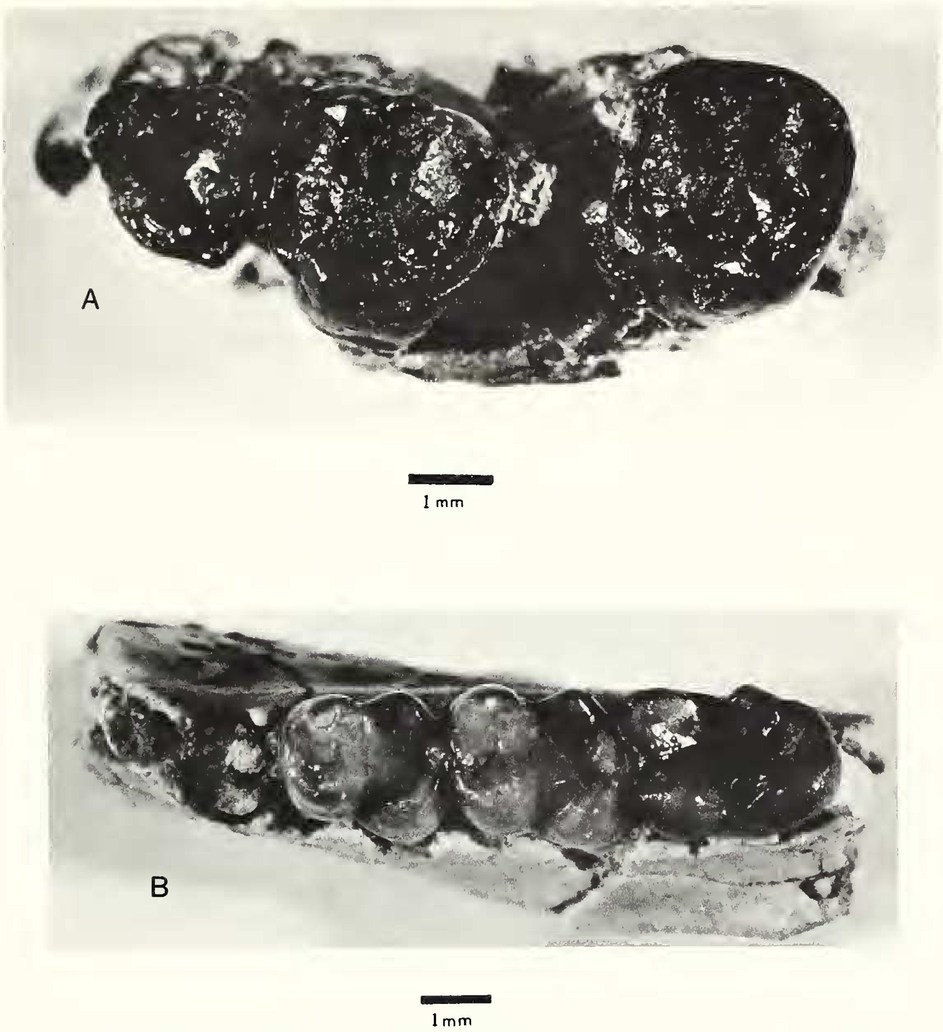


Fig. 11.—Cheek teeth of *Reithroparamys debequensis.* A) LdP^4–M^2, FMNH P 26151. B) LM$_1$–M$_3$, FMNH P 26726 (holotype).

tinct conules. The paracone and metacone are equal in height, the metacone is slightly more buccal than the paracone. The metaconule is larger than the protoconule. A minute mesostyle is present on the tooth. A distinct hypocone is posterior to the protocone. Both posterior and anterior cingulum run the entire width of the tooth.

The upper molar is relatively wider than is typical for reithroparamyines. The conules are relatively large. The protoloph and metaloph converge lingually at the protocone. A relatively large hypocone is present and positioned posterior and lingual to the protocone. The posterior cingulum runs buccally from the hypocone to the buccal margin of the tooth. The anterior cingulum originates at the buccal margin of the base of the protocone and runs to the buccal margin of the tooth. There is a minute mesostyle present on only one of the two known upper molars (UW 15009).

The protoloph and anterior cingulum of M^3 resemble those of the anterior upper molars. The tooth is expanded posterobuccally and reduced posterolingually, giving the tooth a nearly triangular occlusal outline. The metacone is absent, but the metaconule is quite large and part of the remaining metaloph which is a low, narrow loph that runs from the protocone to the posterobuccal margin of the tooth. There is a minute hypocone present, but it is more buccally placed than the protocone. The posterior cingulum runs the entire width as the tooth.

Discussion.—*Reithroparamys ctenodactylops* is clearly referable to this genus based on the presence of a partial hypolophid and isolation of the entoconid on the lower molars, relatively large hypocone on the upper molars, and submolariform P^4 with a distinct hypocone. It differs from other species of *Reithroparamys* in its smaller size, relatively shorter upper molars, larger conules and hypocone on the upper molars, hypocone being more lingually placed, and having the hypoconulid on the lower molars relatively larger and connected to the hypoconid only by a weak posterolophid. All of the features that distinguish *R. ctenodactylops* from other *Reithroparamys* are features present in early ctenodactyloids from Asia (Dawson et al., in press) and may represent the primitive dental morphology for rodents. Therefore, *R. ctenodactylops* represents the earliest and most primitive species of the genus.

Reithroparamys debequensis Wood, 1962
(Fig. 11)

Type specimen.—FMNH P 26726, left mandible with M_1–M_3.

Horizon and locality.—Type from Cherard Park, "about five miles southwest of Rifle, Colorado" (Wood, 1962:134), Lysite equivalent, Debeque Formation, Colorado. Referred specimens from the Knight Member, Wasatch Formation, Wyoming; and possibly Lysite equivalent, Willwood Formation, Wyoming.

Age.—Middle and late early Eocene (Lysitean and Lostcabinian).

Referred specimens.—USNM 22380 (from Knight Member, Wasatch Formation), FMNH P 26151 (from Debeque Formation) and possibly YPM 16525 (from Willwood Formation).

Discussion.—The lower molars of this species have been adequately described by Wood (1962). One specimen referred by Wood to *R. debequensis* (FMNH P 26503) from the same area as the holotype has been designated above as the type specimen of *Notoparamys arctios.* Wood (1962) also referred a maxilla with dP^4–M^2 from the Lysite equivalent of the Debeque Formation (FMNH P 26151) to *Paramys francesi.* Guthrie (1971) noted that this specimen was larger than any of the upper dentitions of *P. francesi* from the Wind River Basin and suggested that this specimen should be referred to *P. excavatus.* The molars of FMNH P 26151 differ from those of *P. excavatus* in being smaller and having the conules more lingually placed. The lingual portion of P^4 is present beneath dP^4 in FMNH P 26151. A distinct hypcone is present posterior to the protocone. All of the above features more nearly approach the condition in *Reithroparamys.* This specimen is referred here to *R. debequensis.*

An additional specimen (YPM 16525), here referred to *Reithroparamys* cf. *R. debequensis,* has been recovered from the Lysite level of the Willwood Formation in the Bighorn Basin. YPM 16525 consists of a nearly complete mandible with M_3. This specimen differs from the type of *R. debequensis* in being slightly larger and having the masseteric fossa terminate anteriorly below the posterior margin of M_1, farther forward than in *R. debequensis.* The masseteric crest and a strong chin process on YPM 16525 are very heavy and reminiscent of the mandible of *R. huerfanensis.*

Reithroparamys huerfanensis Wood, 1962

Type specimen.—AMNH 17031, left mandible with P_4–M_3 and some associated postcranial bones.

Horizon and locality.—Type locality X (see Robinson, 1966), Upper Huerfano Formation, Colorado. Referred specimens from Cathedral Bluffs Tongue, Wasatch Formation, Wyoming and Bridger Formation, Wyoming.

Referred specimens.—FMNH PM 21215 (from Cathedral Bluffs Tongue); UW 1328, FMNH PM 21047, FMNH PM 15155 (from Bridger Formation).

Discussion.—No additional specimens of *Reithroparamys huerfanensis* have been recovered since West's (1973) description of specimens from the Cathedral Bluffs and Bridger Formation. The very heavy knob on the side of the mandible of the holotype is not present on the referred material. Hence, the presence of this knob cannot be included in the diagnosis of this species (see Wood, 1962:136) because it is obviously an anomaly on the holotype.

Reithroparamys huerfanensis was described by Wood (1962) as having an angle of the mandible that was "considerably inflected" and most closely approached the hystricognathous condition. As discussed earlier, the condition in the mandible of *R. huerfanensis* is the result of a heavy chin process and the masseteric fossa bounded by a heavy ridge and not lateral displacement of the mandibular angle. Therefore, *R. huerfanensis,* like all other reithroparamyines, is not hystricognathous and not related to later South American rodents.

Acritoparamys, new genus

Type species.—*Acritoparamys francesi* (Wood, 1962).

Range.—Early to middle Eocene of Wyoming and Colorado.

Referred species.—*A. atwateri* (Loomis, 1907), *A. atavus* (Jepsen, 1937), *A. wyomingensis* (Wood, 1959*a*), and *A. pattersoni* (Wood, 1962).

Diagnosis.—Small rodents; posterior margin of the anterior root of the zygoma level with the center

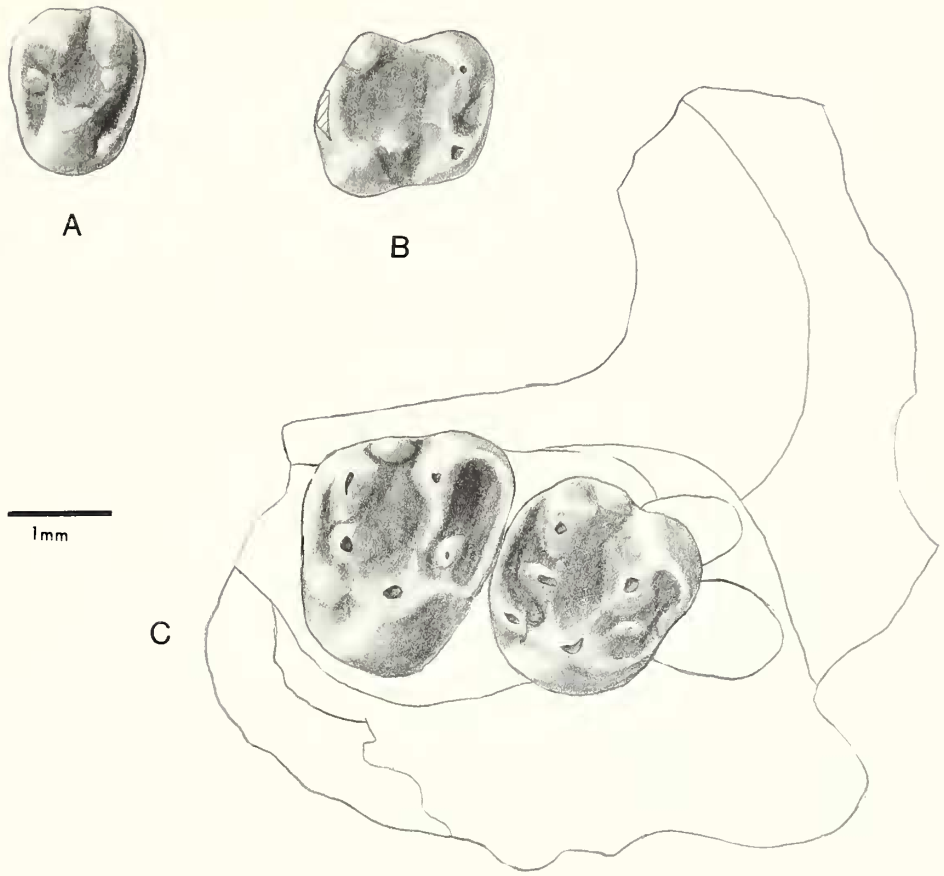


Fig. 12.—Cheek teeth of *Acritoparamys atavus* and *A. francesi*. A) *A. atavus*, LP^4, AMNH 22195. B) *A. atavus*, RM_2, PU 14220 (holotype). C) *A. francesi*, RP^4–M^1, CM 38727.

of P^4; masseteric fossa on the mandible terminates below center or anterior half of M_2; second minute mental foramen present on the mandible below the posterior root of P^4, posterior and ventral to the larger mental foramen; P^4 submolariform with protoconule and small hypocone; M^1 nearly square and equal in size to M^2; large buccolingually elongate hypoconulid present on lower cheek teeth, separated from the entoconid by a distinct groove and attached to the hypoconid by a low ridge; mesoconid small on lower molars; metaconid largest cusp on P_4 with reduced protoconid.

Etymology.—arctios, Greek, mixed or confused.

Comparisons.—Acritoparamys most closely resembles *Reithroparamys* among reithroparamyines, but differs from it by the lack of an entoconid crest that runs buccally into the talonid basin of the lower molars, having less well developed lophs on the cheek teeth, and having a less molariform P^4. *Acritoparamys* differs from *Microparamys*, *Lophiparamys*, and *Apatosciuravus* (described below) by having a relatively smaller hypocone on the upper molars, a more posterior position of the anterior root of the zygoma, and better developed hypoconulid and more isolated entoconid on the lower cheek teeth. *Acritoparamys* also lacks the separation of the anterior cingulum of the lower molars present in *Microparamys* and *Lophiparamys*. *Lophiparamys* also has minute crenulations on the basins of the cheek teeth not present in *Acritoparamys*.

Acritoparamys differs from all other ischyromyids by the features listed above in the diagnosis for the Reithroparamyinae.

Acritoparamys atavus (Jepsen, 1937)
(Figs. 12a, b)

Paramys atavus Jepsen, 1937.

Type specimen.—PU 14200, RM_2.

Horizon and locality.—Type and all referred specimens from Eagle Coal Mine, Bear Creek, Montana.

Age.—Latest Paleocene (Tiffanian).

Referred specimens.—AMNH 22195 (LP^4), and PU 14200c, AMNH 22155, AMNH 22156, AMNH 22163, AMNH 22166, AMNH 22199, CM 11552, CM 11690 (all incisors).

Emended diagnosis.—Smallest species of the genus; hyopconulid only weakly separated from entoconid on M_2; accessory loph runs buccally from the metaconid into the trigonid basin.

Discussion.—Only three additional incisors (CM 11552, CM 11690) can be added to the known record of this species. The two known cheek teeth of *Acritoparamys atavus* have been fully described elsewhere (Jepsen, 1937; McKenna, 1961; Wood, 1962). The presence of a hypocone and protoconule on P^4 and a distinct groove separating the posterolophid from the entoconid on M_2 distinguishes this species from *Paramys.* The enlarged hypoconulid on M_2 is known for *P. taurus,* but is also characteristic of *Acritoparamys.* Based on the morphology of the M_2 and P^4, *Paramys atavus* is more likely referable to *Acritoparamys.* It differs from all other species of this genus in its smaller size and narrower separation of the entoconid from the posterolophid of M_2.

Rose (1981) referred a number of specimens from the Clarkforkian of the Bighorn Basin to *P. atavus.* However, these specimens are smaller than any referred specimen of *A. atavus,* the trigonids of the lower molars are relatively narrower, and the posterolophid is continuous with the entoconid on the lower molars. The UMMP specimens referred by Rose (1981) to *Paramys atavus* are here identified as a new genus and species (see discussion below of *Apatosciuravus*), thus restricting the known range of *Acritoparamys atavus* to the Tiffanian Eagle Coal Mine.

Recently, Gingerich et al. (1980), Krause (1980) and Rose (1981) have referred the Bear Creek, Eagle Coal Mine fauna to the earliest Eocene Clarkforkian age. In its intial description by Simpson (1928, 1929*a*, 1929*b*), the Bear Creek fauna was recognized as late Tiffanian, an allocation followed by nearly all later workers. Rose (1981: Table 52) made a detailed faunal comparison of the Bear Creek fauna, and concluded it was Clarkforkian on the basis of the presence of two primates, a rodent, and a hyopsodont condylarth. Reexamination of the evidence shows the following. The rodent *Paramys atavus* (here referred to *Acritoparamys*) is unique to Bear Creek, its reported occurrence in the Clarkforkian of the Bighorn Basin is based on a misidentification by Rose (1981). The two primates, *Carpolestes nigridens* and *Plesiadapis dubius* are considered to be Clarkforkian species (Gingerich, 1976; Rose, 1975, 1981). The first primate, *C. nigridens,* is clearly present in both the Bear Creek locality and the Clarkforkian of the Bighorn Basin. However, this species may not be exclusively Clarkforkian because of referred material from Wasatchian localities (see Rose, 1981:62–63). The recognition of the other primate is quite tenuous. *Plesiadapis dubius* from Bear creek was originally identified as an indeterminate species of *Plesiadapis* (Simpson, 1928), based on a single isolated M_3. Gingerich (1976) referred this specimen to the Clarkforkian species *P. dubius* rather than the Tiffanian *P. fodinatus.* The only differences recognized by Gingerich between these two species were size, absence of a premolar, and morphology of the upper molars. The M_3 from Bear Creek (AMNH 22154) is well within the size range of *P. fodinatus* (Gingerich, 1976: Tables A-10, A-11) and larger than any specimens referred by Rose (1981: Table 12) to *P. dubius* from the Clarkforkian. The other features separating these two species of *Plesiadapis* cannot be applied to the known material from Bear Creek. Based on size, AMNH 22154 is closer to the Tiffanian *P. fodinatus* than the Clarkforkian species, but no specific identification can be made on such limited material.

Rose (1981) identified five specimens from Bear Creek as *Haplomylus* cf. *simpsoni* that were smaller than *H. simpsoni* from the Clarkforkian in the Bighorn Basin. Elsewhere, *Haplomylus* is only known from the earliest Eocene. If Bear Creek were Tiffanian, this would represent the earliest known specimens of this genus. Conversely, if Bear Creek were earliest Eocene, other animals in the fauna such as *Aphronorus,* would be the latest known representatives of otherwise Paleocene mammals.

Rose (1981: Table 52) compared the Bear Creek fauna with the fauna from a typical Clarkforkian locality (UMMP locality SC-188). He listed 43 species. Only seven of these are common to both localities. One is only identified to genus (*Dissacus*), one is misidentified from SC-188 (*Paramys atavus*), one is not clearly conspecific (*Haplomylus* cf. *simpsoni*), and three species are also known from the Tiffanian and/or Wasatchian outside the Bighorn Basin (*Phenacolemur pagei, Leipsanolestes siegfriedti, Phenacodus primaevus*). Only one species,

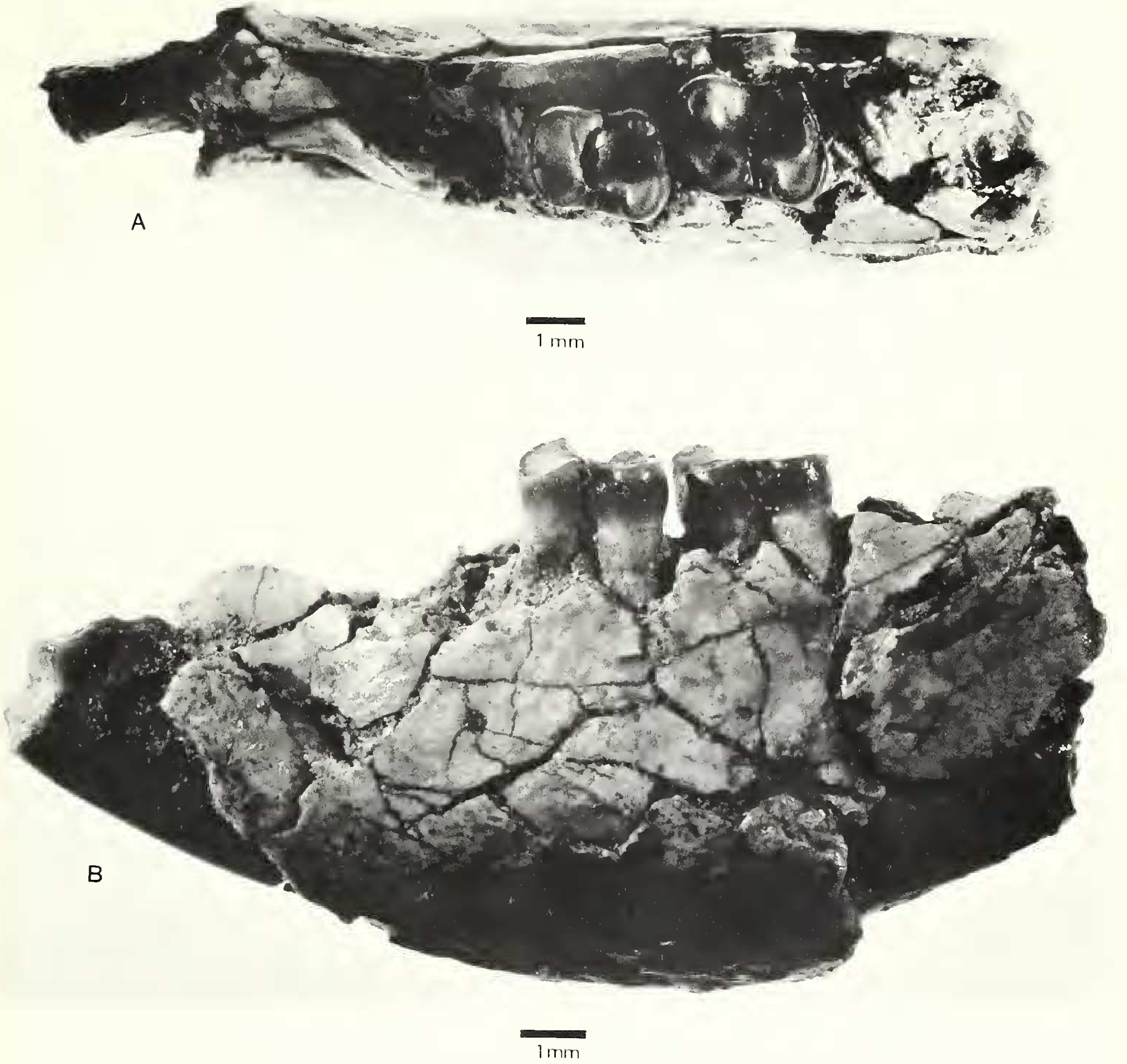


Fig. 13.—Holotype of *Acritoparamys atwateri*, ACM 180. A) Occlusal view of M_1–M_2. B) Lateral view of the mandible.

Carpolestes nigridens, is known only from both the Clarkforkian of the Bighorn Basin and Bear Creek. The possible occurrence of this species in the Wasatchian of the Bighorn Basin (Rose, 1981:62) and lack of it elsewhere outside the Bighorn Basin, may indicate that this species is regionally restricted rather than temporally restricted, as suggested by Rose (1975, 1981).

Overall, the Bear Creek fauna is more likely a unique late Tiffanian fauna as was originally suggested (Simpson, 1928, 1929*a*, 1929*b*; Jepsen, 1937) than a Clarkforkian one. The allocation of this fauna to a Clarkforkian age is questionable at best. The acceptance of a Tiffanian age for the Bear Creek fauna maintains *Acritoparamys atavus* as the earliest known rodent.

Acritoparamys atwateri (Loomis, 1907)
(Figs. 13, 14, Table 5)

Paramys atwateri Loomis, 1907.

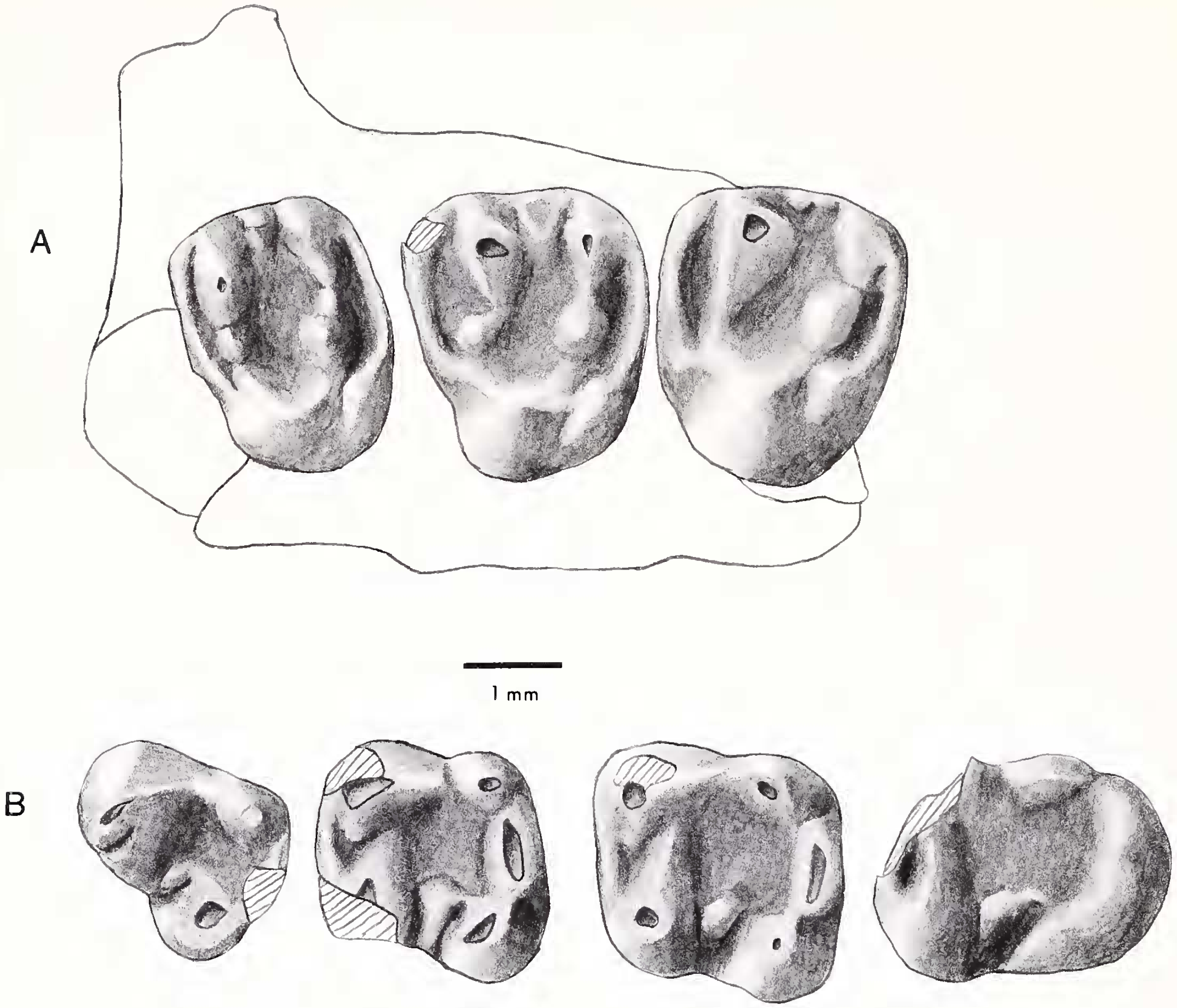


Fig. 14.—Cheek teeth of *Acritoparamys atwateri.* A) LP^4–M^2, AMNH 15710. B) LP$_4$–M$_3$, PU 18410.

Reithroparamys atwateri (Loomis) Wood, 1962.
Paramys annectens Rose, 1981.

Type specimen.—ACM 180, left mandible with M$_1$–M$_2$.

Horizon and locality.—Type from "foot of Tatman Mt." (Loomis, 1907:127), Willwood Formation, Wyoming. Referred specimens also from the Willwood Formation, and Wasatch Formation (Four Mile fauna), Colorado.

Age.—Earliest Eocene (Clarkforkian and Graybullian).

Referred specimens.—CM 12245, PU 18410, PU 19526, ROM 2180, UMMP 71177, AMNH 15710, USNM 19188, USNM 19189, and several unnumbered specimens from AMNH.

Emended diagnosis.—Small size; cusps on lower molars less bulbous than *A. francesi;* posterior arm of protoconid on molars extends lingually, nearly to the base of the metaconid; hypoconulid separated from entoconid by narrow valley.

Description.—The posterior margin of the anterior root of the zygoma is level with the center of P^4, just slightly more posterior than in *Acritoparamys francesi* (described below). P^4 is distinctly smaller than M^1 and shorter than that of *A. francesi.* The anterior cingulum is closely appressed to the protoloph. A minute mesostyle is present. The hypocone is larger than that of *A. francesi.* The protoconule is anterior to the paracone. The upper molars resemble those of *A. francesi* but do not have an enlarged metaconule or parastylar area on M^1 as in the latter.

The masseteric scar on the mandible extends anteriorly to below the middle of M$_2$. A doubled mental foramen is present as in all other species of the genus. The lower incisor is narrow transversely and flattened anteriorly. On the holotype (ACM 180) the anterior surface is slightly concave.

Table 5.—*Dental measurements of* Acritoparamys atwateri.

Specimen no.	P_4			M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
ACM 180	—	—	—	—	1.95	2.17	—	2.34	2.45	—	—	—
PU 19526 L*	—	—	—	—	—	—	2.30	2.25	2.40	3.10	2.25	2.4
PU 19526 R*	2.00	1.50	1.80	2.20	1.90	2.15	2.35	2.30	2.45	3.10	2.30	2.4
PU 18410	2.12	1.44	1.92	2.32	—	2.29	2.37	2.19	2.44	2.86	—	2.2
CU 12245	—	—	—	—	—	—	2.50	—	2.41	—	—	—
ROM 2180	2.06	1.47	1.87	2.34	1.92	2.18	2.49	2.23	2.40	—	—	—
UMMP 71177*	—	—	—	2.25	1.90	2.15	2.40	2.25	2.40	—	—	—
	P^4			M^1			M^2					
AMNH 15710	2.05	2.65	2.60	2.60	2.90	2.75	2.50	3.00	2.80			

* Measurements taken from Rose (1981).

The metaconid is much larger than the protoconid on P_4 but the difference in the sizes of these two cusps is not as great as in P_4 of *A. francesi*. P_4 is narrower anteriorly. The hypoconulid and posterolophid on the lower cheek of *A. atwateri* are distinct and separated from the entoconid. The mesoconid on the lower molars is a distinct cusp. The posterior arm of the protoconid extends lingually across the tooth, nearly closing off the trigonid basin posteriorly. The posterolophid forms a separate posterolingual lobe on M_3.

Discussion.—*Acritoparamys atwateri* differs from *A. atavus* in greater separation of the entoconid and posterolophid and relatively larger hypoconulid on M_2. P^4 of *A. atwateri* is nearly identical in pattern to that of *A. atavus*, but is substantially larger. *Acritoparamys atwateri* is nearly equal in size to *A. francesi* but differs in having less bulbous cusps, a smaller hypoconulid, longer posterior arm of the protoconid, and shorter P^4.

Loomis (1907) described *Paramys atwateri* based on a single mandible with heavily worn M_1–M_2 (ACM 180). Wood (1962) referred this species to *Reithroparamys* based on the separation of the entoconid from the posterolophid. Guthrie (1971) stated that the specimens referred to *R. atwateri* were just minor variants of *Paramys excavatus*.

The entoconid on M_1–M_2 of ACM 180 is isolated and the hypoconulid is a buccolingually elongate swelling on the posterolophid. These features separate ACM 180 from *P. excavatus* and are characteristic of reithroparamyines. The lack of an entoconid ridge on the molars and the presence of a second mental foramen on the mandible of *R. atwateri* make it referable to *Acritoparamys*.

Both Loomis (1907: Fig. 3) and Wood (1962: Fig. 45a) failed to figure or mention the major transverse crack in both molars of the holotype of *A. atwateri*, which has artificially elongated the teeth (see Fig. 13). Wood's (1962: Table 47) measurements of ACM 180 are not corrected for this elongation. The maxillae referred by Wood (1962) to *Paramys excavatus taurus* (AMNH 15710, USNM 19188, USNM 19189), as discussed previously, are more likely referred to *A. atwateri* (see discussion of *P. taurus*).

Wood (1962) included a mandible with P_4–M_2 from the Graybullian of the Bighorn Basin (ROM 2180) in the hypodigm of *Franimys amherstensis*. Rose (1981) questioned this location because the mandible was from a different level than the type of *F. amherstensis*. This specimen is clearly referable to *A. atwateri* based on size and morphology of the mandible and cheek teeth.

Rose (1981) described a new species, *Paramys annectens*, from the Clarkforkian of the Bighorn Basin, which was intermediate in size and morphology between *Paramys atavus* and *P. excavatus* (referring to *P. excavatus taurus*). However, Rose's specimens are equal in size and identical in morphology to Graybullian specimens of *A. atwateri* and should be referred to this species.

The shallow groove on I_1 of the holotype of *A. atwateri* (see Wood, 1962: Fig. 45b) is not present on any of the referred specimens. The variable occurrence of this feature is present in *Reithroparamys delicatissimus* and in species of *Thisbemys* and *Paramys*. Thus, it is not considered inconsistent for this character to be variable in *A. atwateri*.

One specimen from the Lysite level of the Bighorn Basin (AMNH 15139) and one from the Lysite Member of the Wind River Formation (AMNH 15610) were referred by Wood (1962) to *Paramys francesi* and *Reithroparamys atwateri* respectively. Both of thse specimens are identical to *A. atwateri* in morphology but are slightly larger (see Wood, 1962: Tables 22 and 47). These specimens are here referred to *Acritoparamys* cf. *A. atwateri*.

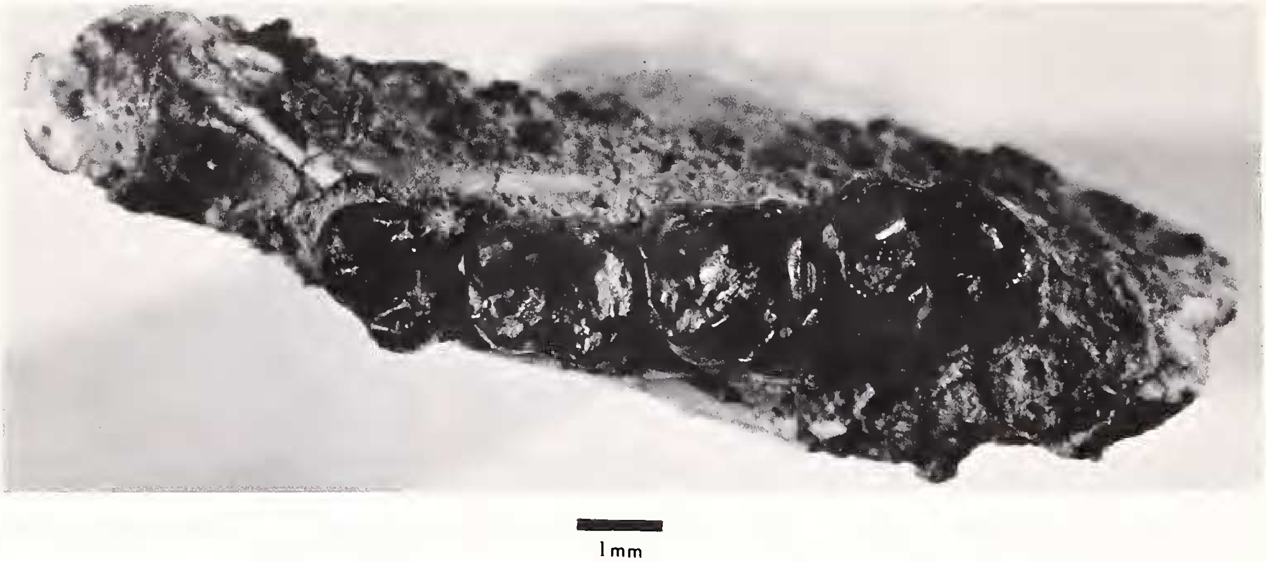


Fig. 15.—Lower dentition of *Acritoparamys francesi*, LP$_4$–M$_3$, CM 37170.

Acritoparamys francesi (Wood, 1962)
(Figs. 12, 15, Table 6)

Paramys francesi Wood, 1962.

Type specimen.—AMNH 14724, left mandible with P$_4$–M$_3$.

Horizon and locality.—Type from locality 1 (see Guthrie, 1971), Lost Cabin Member, Wind River Formation, Wyoming. Referred specimens also from the Lost Cabin Member, and Knight Member, Wasatch Formation, Wyoming.

Age.—Late Early Eocene (Lostcabinian).

Referred specimens.—CM 21144, 21156, 21157, 21159, 21161, 21163–21166, 21169, 21171, 21933, 22221–22224, 22226–22233, 22249, 22536, 22842, 26511, 26512, 26519, 26521–26524, 26594, 27450, 27451, 29150–29152, 29158, 21965, 30957, 35839, 36509–36516, 36928, 37166, 37167, 37169, 37170, 37173, 37176, 38727–38735, and CU 42200, 42201, 44727, 44846, 44847 (from the Knight Member).

Emended diagnosis.—Small species; cusps on molars bulbous; P^4 nearly equal to M^1 in size; metaconule on P^4–M^2 enlarged, near size of metacone; posterior arm of protoconid on lower molars short, leaving trigonid basin widely open posteriorly; mesoconid minute to absent on lower molars.

Description.—The posterior margin of the anterior root of the zygoma is even with the middle of P^4. A prominent ridge originates buccal to P^3 and parallels the anterior margin of the zygoma, marking the insertion of the masseter muscle. The infraorbital foramen is small and unmodified.

P^3 is small and single rooted. P^4 is relatively large, approaching M^1 in size. The paracone is large and buccolingually elongate. The anterior cingulum is separated from the paracone and extends the entire width of the tooth. It is slightly expanded in the parastylar area making a slight anterior bulge. The protoconule is minute and slightly anterior to the paracone. A hypocone is present but minute. The metaconule is large, nearly equal to the metacone in size. A large mesostyle is present and closely appressed to the metacone and separated from the paracone by a deep valley.

The anterior cingulum on M^1 is expanded in the parastylar area, giving the tooth a convex bulge at the anterobuccal corner. As in P^4, the protoconule is small and positioned close to the protocone. The metaconule is slightly smaller than the metacone. A small mesostyle is present. M^2 is similar to M^1 but lacks the anterobuccal convexity and is slightly longer buccally than M^1. M^3 is unknown.

The masseteric fossa on the mandible ends anteriorly below the posterior margin of M$_1$ or anterior margin of M$_2$. A large mental foramen is present just anterior to P$_4$ only slightly below the alveolar margin. The diastema is shallow and short.

The lower incisor is flattened anteriorly, and the medial and lateral sides are parallel. Medially, the enamel extends about one-quarter of the dorsoventral height of the tooth, and laterally about half of the height.

P$_4$ is variable in shape. It varies in length from slightly less than 100% of the length of M$_1$ to about 50% of the length of M$_1$. A metaconid is large and makes up most of the trigonid. The protoconid is minute and situated low on the posterobuccal slope of the metaconid. The entoconid is isolated in most specimens but is entirely lacking on those specimens in which P$_4$ is markedly shortened. The posterolophid is made up of a distinct enlarged hypoconulid which is connected to the hypoconid by a low loph.

Mesoconids on M$_1$ and M$_2$ are reduced to low anteroposterior lophs connecting the protoconid and hypoconid on some specimens. The hypoconulid on the molars is even more pronounced than in P$_4$, and more distinctly separated from the entoconid. The trigonid basin of M$_1$–M$_2$ is minute, closed anteriorly, and

Table 6.—*Dental measurements of* Acritoparamys francesi *(in millimeters).*

Measurements	N	M	S	V	OR
P_4–M_3	5	9.66	.30	3.1	9.37–10.15
P_4 a–p	17	2.18	.14	6.6	1.81–2.43
tra	18	1.56	.12	7.5	1.37–1.72
trp	18	2.02	.14	7.0	1.82–2.30
M_1 a–p	42	2.34	.07	3.1	2.14–2.47
tra	36	1.94	.11	5.6	1.69–2.12
trp	40	2.20	.11	5.0	1.98–2.37
M_2 a–p	34	2.42	.09	3.7	2.27–2.66
tra	29	2.27	.10	4.5	2.10–2.47
trp	31	2.44	.12	4.7	2.23–2.65
M_3 a–p	11	2.55	.12	4.7	2.35–2.77
tra	9	2.26	.15	6.8	2.00–2.54
trp	9	2.15	.12	5.8	1.96–2.35
P^3 a–p	1	1.05	—	—	—
tra	1	1.09	—	—	—
P^4 a–p	7	2.20	.07	3.1	2.14–2.31
tra	7	2.44	.15	6.3	2.27–2.67
trp	7	2.53	.18	7.2	2.30–2.81
M^1 a–p	9	2.23	.06	2.8	2.13–2.33
tra	8	2.56	.09	3.5	2.41–2.69
trp	8	2.41	.08	3.5	2.28–2.51
M^2 a–p	6	2.30	.06	2.8	2.23–2.41
tra	6	2.52	.06	2.4	2.47–2.61
trp	6	2.34	.08	3.2	2.24–2.44

broadly open posteriorly. The posterior arm of the protoconid is short and low, completely disappearing with wear. M_3 is similar to M_1–M_2 but more elongate. The entoconid is reduced. The posterolophid forms an extra lingual lobe on the tooth.

Discussion.—Acritoparamys francesi differs from all other species of the genus in its more molariform P^4, more bulbous cusps, and wider separation of the posterolophid and entoconid on the lower molars.

Only three specimens of *A. francesi* are known from outside the type area of the Lost Cabin Member of the Wind River Formation. All three are from the Knight Member of the Wasatch Formation of southwestern Wyoming (USNM 19302, 22436, 22440), some of which have been previously referred to *Paramys excavatus* (Wood, 1962). These specimens do not differ from the topotypic material of *A. francesi* except in being slightly larger.

Guthrie (1971) suggested that *A. francesi* was ancestral to *Paramys wyomingensis* (here referred to *Acritoparamys*). This does not appear tenable at present because P^4 of *A. francesi* is already more advanced than in *A. wyomingensis* and the separation of the entoconid and posterolophid is not as wide in *A. wyomingensis*.

The Bridgerian *Paramys wyomingensis* is clearly referable to *Acritoparamys* based on the morphology of P^4 and the upper molars as described by Wood (1959*a*, 1962) and West (1969). The lower molars referred by West (1973) to *P. wyomingensis* have a distinct hypoconulid and a separation between the entoconid and posterolophid as in *Acritoparamys*. A maxilla with P^4–M^3 of *P. wyomingensis* (AMNH 97808) recovered from the same area as the holotype of the species has the posterior margin of the anterior root of the zygoma level with the middle of P^4, again, as in *Acritoparamys*. *Paramys wyomingensis* agrees with *Acritoparamys* in all features of the dentition. Hence, this species should be allocated to the latter genus as a distinct species.

Acritoparamys pattersoni (Wood, 1962)

(Fig. 16)

Reithroparamys pattersoni Wood, 1962

Type specimen.—FMNH P 26884, left mandible with P_4–M_1.

Horizon and locality.—Type and referred specimens from "southwest of Rifle, Colorado" (Wood, 1962:135), Lost Cabin equivalent, Debeque Formation, Colorado.

Age.—Late early Eocene (Losteabinian).

Referred specimens.—FMNH P 26642, P. 26787, PM 258.

Discussion.—Acritoparamys pattersoni differs from all other species of the genus in its larger size, more molariform P_4, and doubled metaconule on the upper molars. The metaconid on P_4 of *A. pattersoni* is relatively smaller than in other species and the protoconid is nearly equal to it in height. The only known upper molar of *A. pattersoni* was figured by Wood (1962: Fig. 45j). It closely approaches *Reithroparamys delicatissimus* in having a multiple metaconule.

Guthrie (1971) considered *R. pattersoni* a junior synonym of *Paramys excavatus*, based on on the sample of *P. excavatus* from the Lost Cabin Member of the Wind River Formation. He stated that all specimens of *R. pattersoni* were just minor variants of *P. excavatus*. Clearly, the specimens referred by Wood (1962) to *R. pattersoni* from the Lost Cabin beds of the Wind River Basin are referable to *Paramys*. However, the type and topotypic material of *A. pattersoni* from the Debeque Formation are dis-

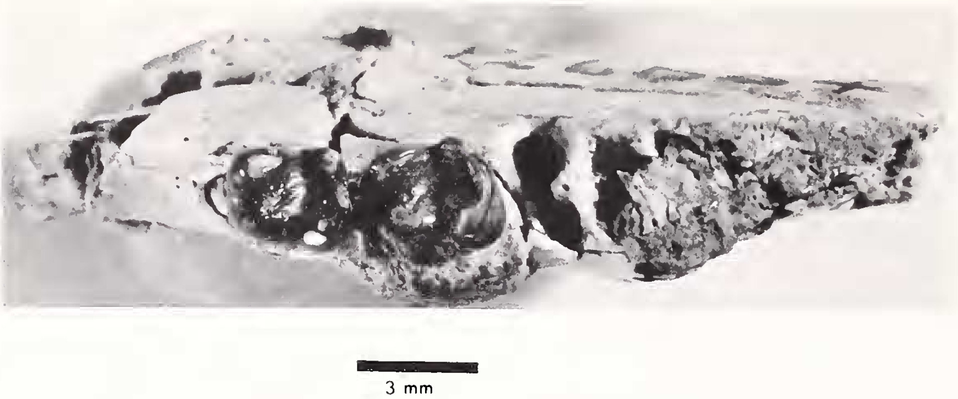


Fig. 16.—Holotype of *Acritoparamys pattersoni*, LP$_4$–M$_1$, FMNH P 26884.

tinct from *Paramys* and agree in molar and mandibular morphology with *Acritoparamys*.

Microparamys Wood, 1959*a*

Type species.—*Microparamys minutus* (Wilson, 1937).

Discussion.—Wood (1959*a*, 1962) diagnosed *Microparamys* as having a large infraorbital foramen. However, the infraorbital foramen in the only partial skull of *Microparamys* (described below) is not larger than is typical for early ischyromyids or sciuravids. The only feature that needs to be added to Wood's diagnosis is that the posterior margin of the anterior root of the zygoma is level with the anterior margin of P^4, farther forward than in any other ischyromyids, and similar to that in many sciuravids.

Wood (1959*a*) initially included two species from North America in *Microparamys*, *M. minutus* and *M. wyomingensis*. In his overall review of early ischyromyids, Wood (1962) recognized four additional species, *M. tricus* (Wilson, 1940) and three new species, *M. lysitensis*, *M. cathedralis*, and *M. wilsoni*, along with four indeterminate species (called sp. A, B, C, D). Dawson (1966) referred *Sciuravus dubius* (Wood, 1949) to *Microparamys*, and Wood (1974) named a new species from the early Oligocene of Texas, *M. perfossus*.

Dawson (1968*b*) questioned the inclusion of *M. wilsoni*, *M. lysitensis*, *M. cathedralis*, *M. wyomingensis*, and *Microparamys* sp. B in the genus. She identified the two specimens referred by Wood (1962) to *Microparamys* sp. C as *Sciuravus eucristadens*. West (1969), based on additional specimens, referred *M. wyomingensis* to *Paramys*. This species has been referred above to *Acritoparamys*. Guthrie (1971) referred both *M. lysitensis* and *M. cathedralis* to *Knightomys depressus*, and *Microparamys* sp. A to *Paramys*. Rose (1981) referred *Microparamys* sp. A to *Paramys atavus*.

The North American species of *Microparamys* accepted here are *M. minutus*, from the middle Eocene, *M. tricus*, *M. dubius*, and *Microparamys* sp. D, from the late Eocene, *M. perfossus*, from the early Oligocene, and two new species from the early Eocene, *M. reginensis* and *M. scopaiodon* (described below). The remainder of the North American species of *Microparamys* described earlier can be referred elsewhere, as follows: *M. lysitensis* and *M. cathedralis* = *Knightomys depressus*; *M. wyomingensis* = *Acritoparamys wyomingensis*; *Microparamys* sp. A = *Apatosciuravus bifax* (new genus and species); *Microparamys* sp. B = *Knightomys huerfanensis* (previously called *Paramys huerfanensis* by Wood, 1962); *Microparamys* sp. C = *Sciuravus eucristidens*; and *Microparamys wilsoni* = *Mysops*.

Microparamys reginensis, new species
(Fig. 17b, Table 8)

Type specimen.—CM 38762, right mandible with M$_2$–M$_3$.

Horizon and locality.—Type from CM locality Almagre # 2 (precise locality on file at CM), Almagre Member, San Jose Formation, Sandoral County, New Mexico. Referred specimen from CM locality Almagre #4 (same horizon as type).

Age.—Middle or late early Eocene (Lysitean or Lostcabinian).

Referred specimen.—CM 38763, LM$_2$–M$_3$.

Diagnosis.—Smallest species of the genus; M$_2$ square in occlusal outline; anterior cingulum separated from protoconid on M$_2$–M$_3$ by narrow valley

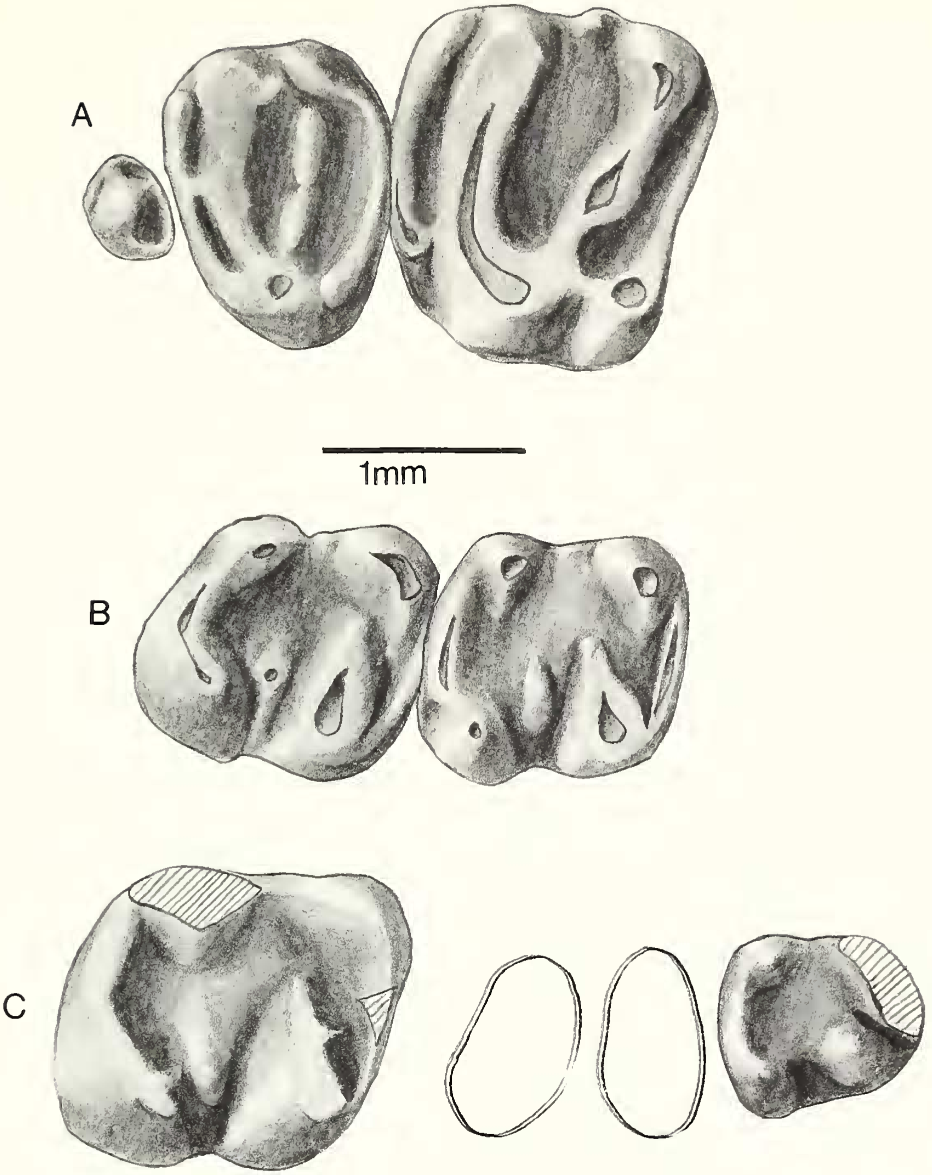


Fig. 17.—Holotypes of *Apatosciuravus* and *Microparamys*. A) *Apatosciuravus bifax*, LP^3–M^1, CM 38765. B) *Microparamys reginensis*, RM$_2$–M$_3$, CM 38762. *M. scopaiodon*, RP$_4$, M$_2$, CM 36196.

which disappears with wear; mesoconid small and anteroposteriorly compressed; minute metastylid on lower molars.

Etymology.—Specific name for Regina, New Mexico, near where the type was recovered.

Description.—*Microparamys reginensis* is the smallest North American species of this genus described. The mandible is slender and the masseteric fossa extends anteriorly to below the posterior root of M$_1$. Two mental foramina are present. The larger anterior foramen is situated high on the mandible below the anterior margin of P$_4$. The second minute foramen is placed more ventrally on the mandible than the first and is below the anterior root of P$_4$.

From the alveoli, it is apparent that P$_4$ is smaller than M$_1$. M$_2$ appears to be larger than M$_1$. The anterior cingulum on M$_2$–M$_3$ is separated from the protoconid by a minute valley which disappears with wear. The posterior arm of the protoconid runs directly lingually across the tooth nearly closing off the trigonid basin posteriorly. A small isolated mesoconid is present and is slightly anteroposteriorly compressed, extending lingually into the talonid basin. The posterior cingulum connects to the entoconid on M$_2$. A minute metastylid is present on the posterolingual slope of the metaconid. This cuspule is eliminated on the referred specimen due to heavy wear.

The lower incisor is narrow, parallel sided and convex anteriorly. Enamel extends about one-third the dorsoventral height of the incisor on the lateral surface, and only very slightly onto the medial surface.

Discussion.—*Microparamys reginensis* is smaller than any other species of the genus. The anterior cingulum does not terminate buccally as a small cuspule as in *M. minutus* and other later species. The lingual extension of the mesoconid on the lower molars of *M. reginensis* is present only on one other species of *Microparamys* (described below as new species). The M_2 and especially M_3 of *M. reginensis* are more nearly rectangular in occlusal outline, as opposed to rhomboidal, than in other species of *Microparamys.*

Microparamys scopaiodon, new species
(Fig. 17c, Table 8)

Type specimen.—CM 36196, right mandible with P_4 and M_2 with associated upper molar.

Horizon and locality.—Hackberry Hollow, Willwood Formation, Wyoming.

Age.—Early early Eocene (Graybullian).

Diagnosis.—Near size of *M. minutus*; P_4 markedly smaller than molars; occlusal pattern of P_4 simple, cusps reduced to isolated cuspules; anterior cingulum short and separated from protoconid on M_2; molars moderately lophate; posterolophid separated from entoconid by narrow groove; posterior arm of protoconid parallel to anterior cingulum to the base of the metaconid; no ectolophid present on M_2; mesoconid anteroposteriorly compressed.

Etymology.—*scopaios*, Greek, dwarf; *odon*, Greek, tooth.

Description.—A single upper molar (M^1 or M^2) of *Microparamys scopaiodon* is preserved in the holotype. Because the specimen has been exploded by a concretion, this tooth cannot be prepared without destroying it entirely. The only observable feature of the upper molar is that there is no distinguishable protoconule on the protoloph. The length of the tooth can be measured (a–p = 1.32 mm).

The masseteric fossa on the mandible ends anteriorly below the posterior end of M_1 or anterior end of M_2. A single mental foramen may be present below the anterior extent of P_4. This area is badly damaged in the holotype, so the presence of any accessory foramina cannot be determined.

P_4 is very small and single rooted. It is more reduced relative to the molars than in any other species of *Microparamys.* All of the major cusps on P_4 (metaconid, protoconid, entoconid, hypoconid) have been reduced to small isolated marginally placed cuspules. The top of the metaconid is broken away, but from the size of the base of this cusp, it is the largest on P_4. It is placed just slightly anterior to the protoconid, and is separated from the latter by a narrow but relatively deep valley. There is no trace of a mesoconid or ectolophid. The posterior cingulum is the only recognizable loph on P_4. It is separated from the entoconid by a groove. The anterior width is narrower than the posterior width.

Only the alveolus for M_1 is preserved in CM 36196. M_1 is distinctly larger than P_4 but smaller than M_2. The anterior cingulum on M_2 is relatively short, arising from the metaconid and running buccally even with the apex of the protoconid. The posterior arm of the protoconid is a pronounced loph running approximately parallel with the anterior cingulum, ending lingually at the base of the metaconid. The anterior cingulum is separated from the posterior arm of the protoconid by a deep valley. The mesoconid is also quite distinct and anteroposteriorly compressed, extending into the talonid basin. The posterolophid originates from the hypoconid and is separated from the entoconid by a distinct groove. A relatively broad hypoconulid is present on the posterolophid. Only the roots of M_3 are preserved in the holotype. It appears that M_3 is longer but narrower than M_2.

The lower incisor is narrow, convex anteriorly, and gently convex on its lateral surface. Enamel extends posteriorly about one quarter of the dorsoventral height of the tooth on the medial side and approximately half of the height on the lateral side.

Discussion.—*Microparamys scopaiodon,* though clearly referable to *Microparamys,* shows great similarity of the middle Eocene genus of sciuravid *Pauromys* Troxell (1923). The height of the lophs on the molars, reduction in size of P_4, anteroposterior compression of the mesoconid on M_2, entoconid separated from the posterolophid, and protoconid isolated with a long posterior arm that runs to the base of the metaconid paralleling the anterior cingulum on *M. scopaiodon* are similarities with *Pauromys* (see Dawson, 1968*b*; Wood, 1959*b*).

The features that separate *M. scopaiodon* from *Pauromys* appear to be just primitive ischyromyid features. The anterior cingulum of M_2 of *M. scopaiodon* is widely separated from the protoconid, as in *Pauromys* and *Microparamys,* but does not extend as far buccally as it does in either of these genera. The anterior cingulum arises from the metaconid in *M. scopaiodon,* as is typical for *Microparamys,* unlike that of *Pauromys* in which the anterior cingulum runs to the lingual margin of the tooth anterior to the metaconid. *Microparamys scopaiodon* also lacks the hypolophid that runs buccally from the entoconid in *Pauromys* and connects to the center of the posterolophid. The masseteric fossa on the mandible of *M. scopaiodon* does not extend as far forward as in *Pauromys,* resembling *Microparamys* in this feature. In *Pauromys,* a minor loph extends buccally from the metaconid into the valley that separates the anterior cingulum and posterior arm of the protoconid. This feature is not present in *M. scopaiodon.*

P_4 of *M. scopaiodon* is clearly reduced in size and is greatly simplified, having all of the major cusps reduced to small isolated cuspules with no connecting lophs. This relative reduction of the cusps of P_4 is not present in *Pauromys*. P_4 of *M. scopaiodon* has a large single root, whereas in *Pauromys*, P_4 is double rooted.

Microparamys sp. (Debeque)
(Fig. 18a, Table 7)

Referred specimen.—FMNH 624-39, partial skull with RM^1.

Horizon and locality.—Southwest of Rifle, Colorado, Lysite equivalent, Debeque Formation, Colorado.

Age.—Middle early Eocene (Lysitean).

Description.—The position of the anterior root of the zygoma is far anterior of the tooth row, its posterior extent is level with P^3. The ridge marking the attachment of the masseter to the zygoma originates anterobuccal to P^3 and parallels the anterior margin of the zygoma. A small bony swelling is present on the rostrum ventral to the infraorbital foramen. The infraorbital foramen is small and unmodified. The incisive foramina are relatively long and narrow. The premaxillary-maxillary suture is positioned laterally on the palate at the anterior end of the infraorbital foramen, runs medially across the palate with many minute crenulations, then runs directly anterior to the posterolateral margin of the incisive foramen.

The rostrum appears to be relatively deep but narrow, although lateral compression of the skull may have altered the proportions of the skull. Anterior to the base of the zygoma is a broad valley running obliquely across the lateral margin of the rostrum, bounded posteriorly by the masseter scar on the zygoma and anteriorly by a low ridge which runs parallel to the masseter scar of the zygoma, possibly for the attachment of the *masseter superficialis* muscle.

Discussion.—Due to the fragmentary nature of FMNH 624-39, very little can be determined about the skull of *Microparamys* except that it follows the general pattern of early ischyromyid skulls. The infraorbital foramen is proportionally the same size as in other reithroparamyines. The rostrum is relatively shorter than in paramyines, similar to that of *Reithroparamys*.

The unique groove on the lateral side of the palate anterior to the tooth row in FMNH 624-39 is also present on the holotype of *Apatosciuravus bifax* (described below). The small swelling ventral to the infraorbital foramen which marks the anterior wall of the groove is similar to the knob for the attachment of the *masseter superficialis* in sciuromorphous rodents (see Wood, 1974; Korth, 1980).

There is no modification of the ventral side of the zygoma or infraorbital foramen on FMNH 624-39 which would indicate modification of the masseter.

The apparent anterior movement of the zygoma in *Microparamys* may be related to the anterior attachment of the *masseter superficialis*. However, in sciuravids there is no swelling below the infraorbital foramen but the zygoma is at least as far anterior as in *Microparamys*.

Table 7.—*Measurements of upper teeth of* Microparamys *sp. (Debeque) and* Apatosciuravus bifax *(in millimeters).*

Measurements		*Apatosciuravus bifax*			*Microparamys* sp.
		CM 38765			
		L	R	TTM 7992	FMNH 624-39
P^3	a–p	0.38			
	tra	0.56			
P^4	a–p	1.09	1.12	1.22	
	tra	1.41	1.40	1.55	
M^1	a–p	1.52	1.48	1.43	1.44
	tra	1.71	1.70	1.55	1.44
	trp	1.66	1.62	1.60	1.42
M^2	a–p			1.40	
	tra			1.63	
	trp			1.49	
M^3	a–p			1.47	
	tra			1.50	
I^1	a–p	—		2.23	
	tra	1.39		1.16	

FMNH 624039 is equivalent in size to the lower jaws identified as *M. reginensis*. It is impossible to prove that these two mandibles are the same species as FMNH 624-39. Recovery of more material from the Debeque and San Jose Formations is needed before association can be made.

Microparamys sp. (Lost Cabin)
(Fig. 18b, Table 8)

Referred specimens.—CU 44712, CU 44725 (isolated lower molars).

Horizon and locality.—Deadman Butte locality (see Stucky and Krishtalka, 1982), Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Discussion.—Two isolated lower molars from the Lost Cabin Member are quite similar in morphology to the Bridgerian *Microparamys minutus*. The major difference between the Lost Cabin specimens of *Microparamys* and *M. minutus* is in the larger size of the Lost Cabin species. There is no buccal cuspule on the anterior cingulum of the Lost Cabin specimens as in later species of *Microparamys*.

Lophiparamys Wood, 1962

Type species.—*Lophiparamys murinus* (Matthew, 1918).

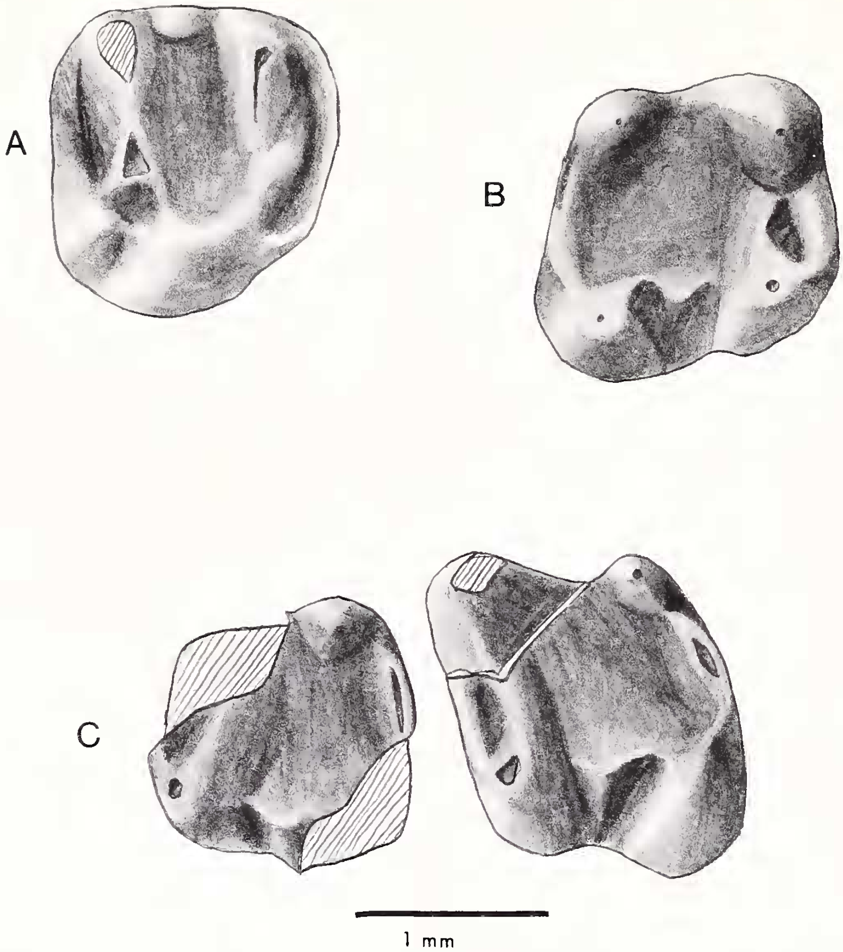


Fig. 18.—Molars of *Microparamys* sp. and an indeterminate reithroparamyine. A) *Microparamys* sp. (Debeque), RM^1, FMNH 624-39. B) *Microparamys* sp. (Lost Cabin), RM_1 or M_2, CU 44712. C) indeterminate reithroparamyine, LM_1–M_2, AMNH 17005.

Lophiparamys murinus (Matthew, 1918)

Paramys murinus Matthew, 1918.
Lophiparamys murinus (Matthew) Wood, 1962.

Type specimen.—AMNH 15131, associated mandibles with LP_4–M_3 and RM_1–M_3.

Horizon and locality.—Willwood Formation, Wyoming.

Age.—Early early Eocene (Graybullian).

Discussion.—The holotype (AMNH 15131) remains the only known specimen of *Lophiparamys murinus.* This specimen has been adequately figured and described elsewhere (Matthew, 1918; Wood, 1962). Nothing has been added to our knowledge of this species since its original description (Matthew, 1918) and subsequent discussion (Wood, 1962).

Lophiparamys debequensis Wood, 1962

Type specimen.—FMNH PM 1217, LM_1.

Horizon and locality.—Type from "confluence of Shooty and Scenery Gulches, seven miles east-northeast of the junction of White River and Piceance Creek, Rio Blanco County" (Wood, 1962:169), Lysite equivalent, Debeque Formation Colorado. Referred specimens from the Lysite Member, Wind River Formation, Wyoming and Almagre Member, San Jose Formation, New Mexico.

Age.—Middle and possibly late early Eocene (Lysitean and possibly Lostcabinian).

Referred specimens.—FMNH PM 1213 (from Debeque Formation); AMNH 48169 (from San Jose Formation); and CM 38709, ACM 2540, ACM 2575 (from Lysite Member).

Discussion.—Previously, *Lophiparamys debe-*

Table 8.—*Measurements of lower teeth of some reithroparamyines (in millimeters).*

	P_4			M_1			M_2			M_3		
Measurements	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
Apatosciuravus bifax												
PU 18419	1.31	0.86	1.07	1.41	—	—	—	—	—	—	—	—
CM 36643	—	—	—	1.48	1.24	1.49	—	—	—	—	—	—
ACM 10997	—	—	—	—	—	—	1.58	1.55	1.78	—	—	—
WAM 175	—	—	—	1.33	1.11	1.21	—	—	—	—	—	—
UMMP 65244*	1.10	0.85	1.00	—	1.30	—	1.70	1.30	—	1.70	—	—
UMMP 69871*	1.30	0.85	1.20	1.60	1.30	1.60	1.70	1.50	1.70	—	—	—
UMMP 71173*	—	—	—	—	—	1.50	1.65	1.45	1.70	—	—	—
Microparamys scopaiodon												
CM 36196	0.99	0.61	0.79	—	—	—	1.55	1.36	1.40	—	—	—
Microparamys reginensis												
CM 38762	—	—	—	—	—	—	1.19	1.16	1.21	1.30	1.25	1
CM 38763	—	—	—	—	—	—	1.29	—	1.20	1.29	1.18	—
Microparamys sp. (Lost Cabin)												
CU 44712	—	—	—	1.46	1.32	1.50	—	—	—	—	—	—
CU 44725	—	—	—	1.48	1.42	1.53	—	—	--	—	—	—
reithroparamyine indeterminate												
AMNH 17005	—	—	—	—	—	—	1.41	1.47	1.56	—	—	—

* Taken from Rose (1981).

quensis has been reported from the Lysite equivalent of the Debeque Formation (Wood, 1962), Lysite Member of the Wind River Formation (Wood, 1965; Guthrie, 1967), and the Lost Cabin Member of the Wind River Formation (Guthrie, 1971). A mandible with M_2–M_3 (CM 38709) has since been collected from the Lysite Member, Wind River Formation along with a partial mandible with M_3 from the San Jose Formation (AMNH 48169).

The occurrence of *L. debequensis* in the Lost Cabin fauna is questionable. Guthrie (1971:73) cited only two specimens of cheek teeth of *L. debequensis* (CM 22234, CM 22235) from the Lost Cabin fauna by number and figured both of them (Guthrie, 1971: Figs. 14a, 14b). In his tables of measurements, he (1971: Table 19) listed three cheek teeth, a P_4 and two M_3s. According to the measurements given by Guthrie, CM 22235 and the two M_3s are comparable in size to other specimens of *L. debequensis* (see Wood, 1962: Table 57; Wood, 1965: Table 1). However, measurements taken from Guthrie's figures are slightly larger than the measurements given for *L. woodi* (Guthrie, 1971: Table 19), the largest species of the genus.

The two specimens cited and figured by Guthrie, CM 22234 and CM 22235, cannot be found in the Carnegie Museum of Natural History collection. In fact, there is no record in the systematic files at Carnegie Museum of Natural History that these specimens were ever catalogued. Hence, until the specimens cited by Guthrie can be found and their measurements can be matched with either the tables or figures, *L. debequensis* should not be considered as a part of the Lost Cabin fauna.

Lophiparamys woodi Guthrie, 1971

Type specimen.—CM 22241, LM_3.

Horizon and locality.—Type and referred specimens from locality 4 (Guthrie, 1971), Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—CM 22236–22240 (all isolated teeth).

Discussion.—No new material of *Lopiparamys woodi* has been recovered since its original description (Guthrie, 1971). This species differs from *L. murinus* and *L. debequensis* in being larger and having a more finely crenulate enamel surface on the cheek teeth.

Reithoparamyine genus and species indeterminate

(Fig. 18c, Table 8)

Referred specimen.—AMNH 17005, left mandible with M_2 and partial M_1.

Horizon and locality.—Elk Creek, Willwood Formation, Wyoming.

Age.—Early early Eocene (Graybullian).

Description.—AMNH 17005 is a small rodent (Table 8). The masseteric fossa on the mandible terminates anteriorly below the anterior root of M_2. No other features of the mandible can be determined.

M_2 is anteroposteriorly compressed, giving the tooth a transversely elongate appearance. The trigonid is nearly equal in width to the talonid. The trigonid basin of M_1 and M_2 is minute and closed anteriorly and posteriorly. A large, transversely elongate hypoconulid is present on both M_1 and M_2, and the entoconid is isolated from the hypoconulid. The ectoloph is weak.

Discussion.—The anterior position of the masseteric fossa on the mandible, isolated entoconid and enlarged hypoconulid on M_1–M_2 make AMNH 17005 clearly referable to the Reithroparamyinae. The unique feature of AMNH 17005 is the anteroposterior compression of M_2. Only one other ischyromyid has similar proportions of M_2, *Uriscus californicus* Wood (1962) from the late Eocene of California. This does not imply any close relationship between AMNH 17005 and *Uriscus*. *Uriscus* lacks the enlarged hypoconulid of reithroparamyines and the masseteric fossa does not extend as far anteriorly on the mandible.

The occurrence of AMNH 17005 in the Graybullian shows the greater diversity of small *Microparamys*-sized rodents in the early Eocene than was previously known.

Subfamily ?Reithroparamyinae

Apatosciuravus, new genus

Type species.—*Apatosciuravus bifax*, new species.

Range.—Earliest Eocene of Wyoming and Colorado.

Referred species.—Type species only.

Diagnosis.—Small rodents; posterior margin of anterior root of zygoma level with P^3; double mental foramen on the mandible; P_4^4 small relative to molars with distinct hypocone; metaloph and metacone poorly developed on P^4; upper molars cuspate with weak loph development and relatively large hypocones; trigonids of lower molars much narrower than talonids; anterior cingulum continuous with protoconid; small but distinct hypoconulid present on lower cheek teeth.

Etymology.—*apate*, Latin, false; *Sciuravus*, possibly related rodent.

Comparisons.—*Apatosciuravus* differs from *Reithroparamys* and *Acritoparamys* in the more anterior position of the anterior root of the zygoma, less molariform P^4, larger hypocone on M^1–M^2, and less well developed hypoconulid on P_4–M_2. *Apatosciuravus* differs from *Microparamys* and *Lophiparamys* in having a larger hypocone on M^1–M^2 and lacking an anterior cingulum on the lower molars separate from the protoconid. No other reithroparamyine has the buccolingual compression of the trigonids of M_1–M_2 that is present in *Apatosciuravus*. *Apatosciuravus* differs from paramyines, ailuravines and pseudoparamyines by the same features as all other reithroparamyines.

Apatosciuravus bifax, new species
(Fig. 17a, Tables 7, 8)

Microparamys sp. A Wood, 1962.

Type specimen.—CM 38765, partial palate and rostrum with RP^4–M^1 and LP^3–M^1.

Horizon and locality.—Type from Dorsey Creek, Willwood Formation, Wyoming. Referred specimens also from the Willwood Formation and East Alheit Pocket Quarry, Four Mile Fauna, Wasatch Formation, Colorado.

Age.—Earliest Eocene (Clarkforkian to Graybullian).

Diagnosis.—As for genus.

Referred specimens.—TTM 7992, PU 18419, WAM 175, CM 36643 (from Gray Bull beds, Willwood Formation); UMMP 65244, 69219, 29871, 71173, ACM 10997 (from Clarkforkian Willwood Formation); six unnumbered specimens from AMNH (from Four Mile fauna).

Etymology.—*bifax*, Latin, two-faced.

Description.—The position of the anterior root of the zygoma, size of the infraorbital foramen, and presence of a bony knob anterior to the tooth row are identical to that described above for *Microparamys*.

P^3 is minute and single rooted. It has a major central cusp with two very low ridges running posteriorly from it. The lingual ridge runs posteriorly from the lingual edge of the main cusp and curves buccally, defining a small shallow posterolingual basin. The second loph originates from the center of the main cusp and runs posterobuccally.

P^4 is small relative to M^1. The tooth is dominated by four low lophs (anterior cingulum, protoloph, metaloph, posterior cingulum). Both cingula run the entire width of the tooth. The metacone is reduced to a small cuspule at the posterobuccal corner of the tooth. The conules are reduced to minor swellings on the protoloph and metaloph, and cannot be distinguished from the continuous lophs after moderate wear. A small but distinct hypocone is present. The mesostyle is minute.

The molars are also dominated by four low, but continuous transverse lophs. The protoconule is not recognizable on the protoloph of any of the available specimens. A minute metaconule is distinguishable on the metaloph until late stages of wear. The anterior cingulum terminates buccally as a minute cuspule anterior to the protocone. The protoloph and metaloph on M^1–M^2 converge toward the cresentic protocone. A distinct mesostyle is present on the molars.

The anterior cingulum and protoloph of M^3 are similar to those of M^1 and M^2. The metacone is posteriorly and lingually placed, giving the tooth a triangular occlusal outline. The metacone appears to be reduced in size, and the posterior cingulum shortened, but this is difficult to determine because the only known M^3 of *A. bifax* (TTM 7992) is heavily worn in the area.

The upper incisor is long anteroposteriorly and narrow. The anterior surface is slightly convex and the medial and lateral sides are parallel. Enamel extends only slightly onto the lateral side, and does not extend onto the medial side.

The masseteric fossa on the mandible terminates anteriorly below the middle or posterior half of M_2. Mental foramina are preserved on only one specimen (PU 18419). A relatively small mental foramen is present high on the side of the mandible just anterior and ventral to the anterior margin of P_4. A second minute foramen is directly posterior to the first, just posterior to the center of P_4.

Both Wood (1962; as *Microparamys* sp. A) and Rose (1981; as *Paramys atavus*) have adequately described the lower cheed teeth of *A. bifax*. The unique features of the lower cheed teeth are the small P_4, and narrow trigonids of the molars.

Discussion.—*Apatosciuravus bifax* differs from *Microparamys* in not having the anterior cingulum completely separated from the protoconid on the lower molars, having a larger hypocone on the upper molars, lacking a metastylid and having a narrower trigonid on the lower molars. In size, *A. bifax* is approximately equal to the early Oligocene *Microparamys perfossus* Wood (1974).

Apatosciuravus bifax shares many features with both *Microparamys* and sciuravids: 1) anterior position of the zygoma and masseteric fossa on the mandible; 2) hypocone on P^4; and 3) large hypocone on the upper molars. *Apatosciuravus bifax* also has the attachment for what is believed to be the *masseter superficialis* present on the skull of *Microparamys*. The trigonid basin of *A. bifax* is similar to that of the indeterminate reithroparamyine described above.

Wood (1962) originally identified *Microparamys* sp. A from the early Wasatachian (later considered Clarkforkian by Rose, 1981) of the Bighorn Basin based on an isolated molar (ACM 10997), and a partial mandible with a heavily worn M_1 (WAM 175), but noted that there was a difference in the size of the two specimens. Guthrie (1971) referred Wood's *Microparamys* sp. A to *Paramys*, and along with a number of other synonymies, he concluded that the earliest North American species of *Microparamys* did not occur until the Bridgerian.

Rose (1981) referred the isolated molar of *Microparamys* sp. A (ACM 10997) to *Paramys atavus*, along with several more specimens from the Bighorn Basin. As discussed above, all of the material referred by Rose (1981) to *Paramys atavus* except for those from Eagle Coal Mine is here allocated to *A. bifax*. The holotype of *A. bifax* is from the Graybullian. However, the referred Clarkforkian specimens are virtually identical to those from the early Wasatchian, and are referable to *A. bifax*. Though not described by Rose (1981), a mandible of *A. bifax* from the Clarkforkian has an associated upper molar (UMMP 69219) that agrees with the holotype of *A. bifax* in size and morphology.

Subfamily Pseudoparamyinae Michaux, 1964

Included genera.—*Plesiarctomys* Bravard (1850), *Pseudoparamys* Michaux (1964), and *Franimys* Wood (1962).

Discussion.—Michaux (1964, 1968) defined the Pseudoparamyinae on the following dental characters: 1) P^3 absent; 2) P^4 anteroposteriorly compressed; 3) M^1 and M^2 rectangular with protoloph and metaloph parallel; 4) anterior cingulum on lower molars developed; 5) trigonid basins closed; 6) mesoconid transversely elongate; and 7) posterior cingulum continuous with the entoconid. He included the two European genera *Pseuodoparamys* and *Plesiarctomys*. Michaux (1968) also noted the similarity between the P^4 of *Pseudoparamys* and *Franimys*.

Some features of the skull appear to be shared by *Pseudoparamys*, *Plesiarctomys*, and *Franimys*. In all three genera the posterior margin of the anterior root of the zygoma is level with the middle of P^4. It is just slightly more forward in *F. amherstensis*. If Wood's (1970: Fig. 1) reconstruction of the skull of *Plesiarctomys* were correct, it is very similar to that of *Franimys* in having a short broad snout and having the nasals end posteriorly on the same line with the premaxillaries.

In *Franimys*, a single sagittal crest runs the length of the cranium, divides at the level of the posterior margin of the orbits and runs laterally, nearly at right angles to the sagittal crest, to the lateral margin of the skull. In *Plesiarctomys* the anterior extensions of the sagittal crest are gradual but very similar to those in *Franimys*. In manitshines the anterior part of the crest begins laterally perpendicular to the sagittal crest, as in *Franimys*, but turns into a more gradual angle. The split of the sagittal crest of *Paramys delicatus* resembles that of *Franimys*, occurring far forward on the cranium, but the anterior branches of the crest diminish laterally and do not reach the lateral margin of the skull.

The skull of *Franimys* possesses postorbital processes. These are unknown on any other ischyro-

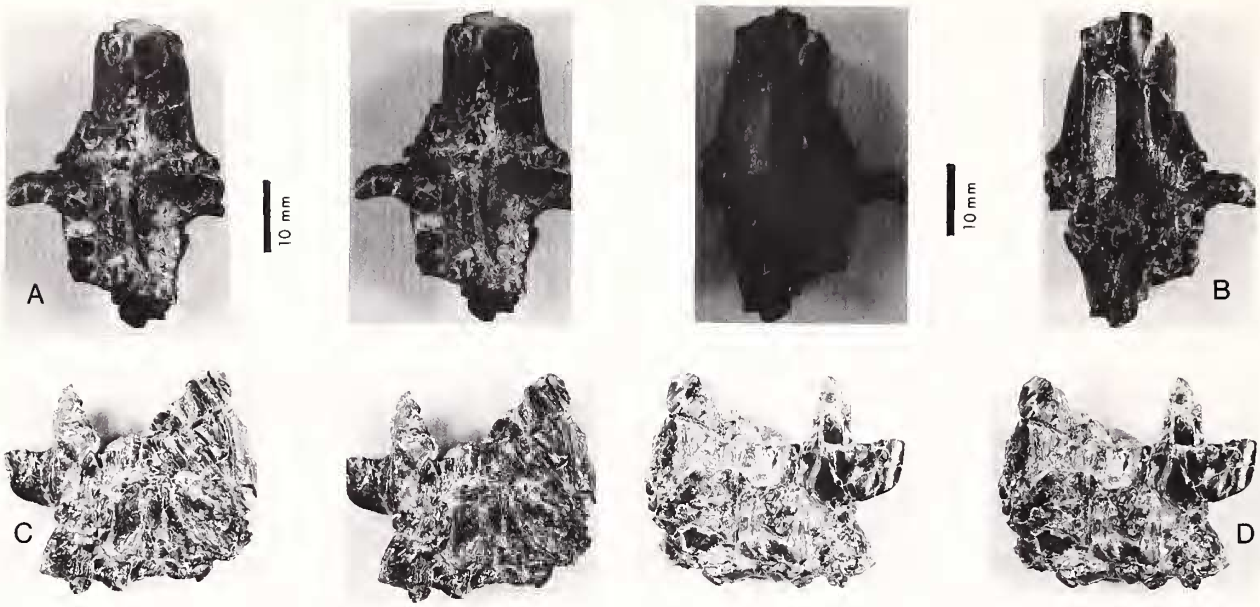


Fig. 19.—Skull of *Franimys amherstensis,* ACM 10524 (holotype). A) Stereophotograph of ventral view of the anterior portion of the skull. B) Stereophotograph of dorsal view of anterior portion of skull. C) Stereophotograph of ventral view of posterior portion of skull. D) Stereophotograph of dorsal view of posterior portion of skull.

myids except the European genus *Ailuravus* (Weitzel, 1949).

Unfortunately, no lower teeth of *Franimys* are known so no comparison can be made with those of *Pseudoparamys.*

P^4 of *Pseudoparamys* is very similar to that of *Franimys* and is two rooted. P^4 of *F. buccatus* has two buccal roots but they do not separate until well below the base of the crown. The new species of *Franimys* (described below) may have two buccal roots but all that can be determined from the known material is that there is an anteroposteriorly elongate buccal root with a central depression at the level of the alveolar margin. Once the root has entered the bone it may well divide into two. The reduction in the number of lingual roots is probably related to the anteroposterior compression of the tooth.

The only known feature of the dentition of *Franimys* that is unlike *Pseudoparamys* is the presence of P^3. However, Wood (1970) showed that in most specimens of *Plesiarctomys,* at least a dP^3 is present, indicating that *Plesiarctomys* lost P^3 independently of *Pseudoparamys.* If this criterion were dropped from Michaux's (1964, 1968) diagnosis, *Franimys* can easily be considered a pseudoparamyine.

Both Wood (1962, 1976*a*) and Black (1971) included *Franimys* in the Reithroparamyinae. However, the morphology of P^4, arrangement of the sagittal crest on the skull, and lack of a bulla ossified to the skull, separate *Franimys* from *Reithroparamys* and the Reithroparamyinae.

Franimys Wood, 1962

Type species.—Franimys amherstensis Wood, 1962.

Range.—Early Eocene of Wyoming and New Mexico.

Referred species.—Franimys buccatus (Cope, 1877) and *Franimys ambos,* new species.

Emended diagnosis.—Small rodents; broad skull with short snout; postorbital processes on the frontals; nasals and premaxillary bones extend posteriorly to the same level; posterior margin of the anterior root of the zygoma level with the center of P^4; P^4 small, narrow, oval in occlusal outline, without a hypocone; hypocone on upper molars small; I^1 disproportionately large.

Franimys amherstensis Wood, 1962
(Figs. 19, 20, 21)

Type specimen.—ACM 10524, skull with RP^4 and M^2–M^3, and mandible without teeth and several postcranial bones.

Horizon and locality.—"100 yards southeast of the northwest corner of Sec. 9, T56N, R101W" (Wood, 1974:17), Willwood Formation, Wyoming.

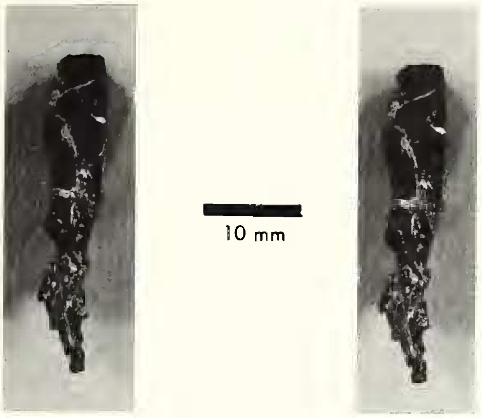


Fig. 20.—Stereophotograph of ventral view of the mandible of *Franimys amherstensis*, ACM 10524 (holotype). Anterior toward the top.

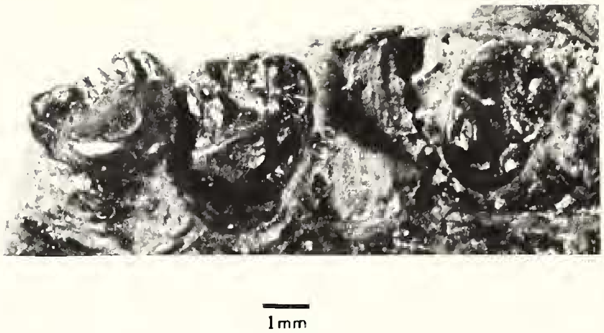


Fig. 21.—Upper cheek teeth of *Franimys amherstensis*, P^4, M^2–M^3, ACM 10524 (holotype).

Age.—Earliest Eocene (Clarkforkian).

Emended diagnosis.—Largest species of the genus; posterior margin of the anterior root of zygoma nearly even with anterior margin of P^4; P^4 very narrow anteroposteriorly and two rooted.

Discussion.—A number of features of the skull and mandible of *Franimys amherstensis* were incorrectly figured by Wood (1962: Fig. 48). The posterior half of the skull (ACM 10524) is so badly crushed that many features are either distorted or impossible to determine. The temporal foramina were figured and described by Wood as being very near the sagittal crest, a unique feature among ischyromyids. However, the fragments of bone which contain these foramina appear to be from near the temporal-squamosal boundary, as in all other ischyromyids, and to have been moved to the central position by crushing of the skull. It is also impossible to determine if an interparietal bone is present, due to extensive crushing.

The only known mandible of the species belongs to the holotype. Wood (1962) described this specimen as being incipiently hystricognathous with the angle of the mandible arising laterally from the side of the mandible. As discussed previously, this specimen is so badly crushed and partially exploded by concretionary deposition between the fragments that the true position of the angle cannot be reconstructed.

P^4 of *F. amherstensis* is anteroposteriorly compressed and two rooted. Most of the buccal margin of the tooth is broken away on the holotype. Wood (1962:142) interpreted this tooth as having a single major loph, the doubled metaloph, a thin anterior cingulum which terminated buccally with a small swelling homologous to the paracone, and a short posterior cingulum. This tooth is in such poor condition in the type that its morphology is very difficult to interpret. The buccal swelling that Wood interpreted as a paracone appears to be a wear facet that has extended onto the side of the tooth. There is no distinct swelling. More importantly, the valley between the metaloph and anterior cingulum on P^4 is a wear facet and not an original valley between these lophs. The small valley in the center of the metaloph interpreted by Wood as the valley between the two metalophs is more likely the wear facet for the metaconule. In all, it is probable that a protoloph was present on P^4 of *F. amherstensis* but has been worn away. The amount of wear on the molars is comparable with that on P^4, and sufficient to have removed the protoloph of P^4. The position and size of the paracone cannot be determined because of wear and breakage of the tooth on the holotype.

Wood (1962) interpreted the morphology of P^4 of *F. amherstensis* as primitive for all rodents. However, most other early ischyromyids have a narrow metaloph with a metacone smaller than the paracone, implying the secondary development of the metacone and metaloph, with the paracone and protoloph being primary. The primary development of the paracone and subsequent development of the metacone on the posterior upper premolars in rodents is also consistent with other orders of mammals such as insectivores and primates.

Even though the morphology of the occlusal surface of P^4 is very poorly known, *F. amherstensis* is distinguishable from other species of *Franimys* by its size and slightly more anterior position of the anterior root of the zygoma.

The upper incisor of *F. amherstensis* is larger in relation to the size of the cheek teeth than in other

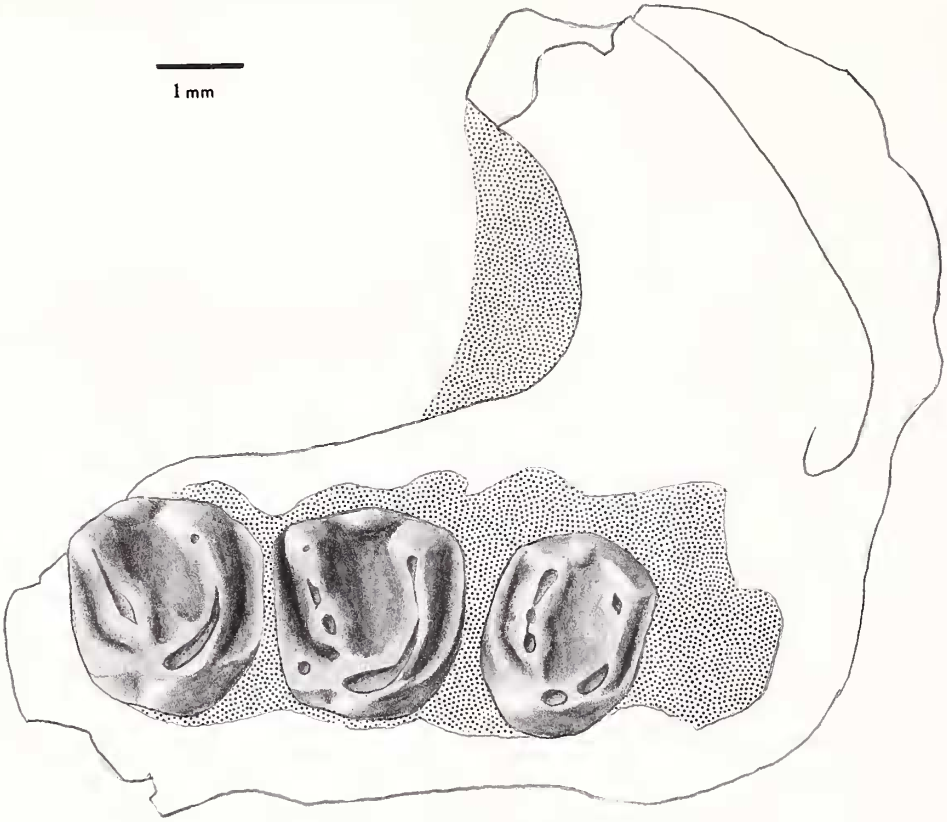


Fig. 22.—Holotype of *Franimys ambos*, RP^4–M^2, CM 37091.

ischyromyids. The enamel on the upper incisors is almost completely restricted to the anterior surface. It does not extend onto the lateral surface as far as in *Paramys copei.*

Franimys buccatus (Cope, 1877)

Plesiarctomys buccatus Cope, 1877.
Paramys buccatus (Cope) Roger, 1896.
?*Sciuravus buccatus* (Cope) Matthew, 1909.
"*Paramys*" *buccatus* (Cope) Wilson, 1949.
Franimys buccatus (Cope) Wood, 1962.

Type specimen.—USNM 1129, right maxilla with P^4–M^2.

Horizon and locality.—Unknown locality, San Jose Formation, New Mexico.

Age.—Probably middle or late early Eocene (Lysitean or Lostcabinian).

Emended diagnosis.—Small species; paracone of P^4 situated near center of the tooth; M^1 distinctly smaller than M^2.

Discussion.—*Franimys buccatus*, like *F. amherstensis*, is known only from the holotype. It differs from the type species in being slightly smaller. Because the occlusal pattern of P^4 of *F. amherstensis* is not clearly known, no comparison can be made with that of *F. buccatus.* The position of the paracone on P^4 of *F. buccatus* is unique among ischyromyids. The much smaller size of M^1 relative to M^2 is also distinctive.

Franimys buccatus is clearly referable to *Franimys* based on its small size, position of the anterior root of the zygoma, and the small oval P^4, lacking a hypocone.

Franimys ambos, new species
(Fig. 22, Table 9)

Type specimen.—CM 37091, right maxilla with P^4–M^2.

Horizon and locality.—Type area of the Lysite Member, Wind River Formation, Wyoming.

Age.—Middle early Eocene (Lysitean).

Diagnosis.—Smallest species of the genus; P^4 with complete protoloph connecting to a buccally positioned paracone; M^1 and M^2 nearly equal in size and squre in outline.

Hypodigm.—Type only.

Etymology.—*ambos*, Greek, rim.

Description.—*Franimys ambos* is smaller than either *F. buccatus* or *F. amherstensis*. The anterior root of the zygoma is slightly more posterior than in the other species, but in all other features of the palate observable, is identical with those of the other species.

P^3 is absent in the holotype but it is evident from the alveolus and wear facet on P^4 that P^3 was small and situated near the center of the anterior margin of P^4.

P^4 is more molariform than in *F. buccatus*. The paracone is nearly at the buccal edge of the tooth. The protoloph connects the paracone to the protocone, but there is no indication of a protoconule on it. A separate wear facet is present on the anterobuccal slope of the protocone but this is not a protoconule. The anterior cingulum runs lingually from the level of the paracone to the level of the apex of the protocone and is closely appressed to the protoloph. The metacone is anteroposteriorly compressed, and the metaconule is double. The lingual metaconule is larger than the more buccal one. The metaloph attaches to the protocone via a low narrow loph. The posterior cingulum originates at the protocone and wraps around the posterior margin of the tooth, ending buccally at the metacone. There is no indication of a hypocone. A small mesostyle is present and placed nearer the metacone than paracone.

M^1 and M^2 are nearly identical in size and proportions. They do not differ from the other species of the genus except for smaller size and apparent lack of a protoconule on the protoloph. Size and position of the hypocone, anteroposterior elongation of the mesostyle and length and arrangement of the cingula and metaloph are identical to those of *F. buccatus* and *F. amherstensis*.

Discussion.—*Franimys ambos* is the smallest species of the genus. M^1 and M^2 of *F. ambos* are nearly identical in size and proportions, unlike *F. buccatus* in which M^1 is markedly smaller than M^2. P^4 of *F. ambos* most closely resembles that of *Pseudoparamys teilhardi* (Michaux, 1968: Pl. 4, Fig. 1). The paracone is situated at the buccal margin of the tooth and there is a complete protoloph, as in *P. teilhardi*. P^4 of *F. ambos* differs from that of *P. teilhardi* in being less compressed anteroposteriorly.

The molars of *F. ambos* are very close in morphology to those of both *F. amherstensis* and *F. buccatus* in having an anteroposteriorly elongate mesostyle, poorly developed protoconule, and small hypocone. No specimens of lower molars from the Lysite Member of the Wind River Basin are comparable in size to the type of *F. ambos*. Therefore, *Franimys* is still known only from upper dentitions.

Subfamily Ailuravinae Michaux, 1968

Included genera.—*Ailuravus* Rütimeyer (1891), *Melidimys* Michaux (1968), and *Mytonomys* Wood (1956).

Table 9.—*Dental measurements of the type specimen of* Franimys ambos *(in millimeters), CM 37091.*

Tooth	a–p	tra	trp
P^4	1.85	2.51	—
M^1	2.23	2.51	2.48
M^2	2.19	2.47	2.31

Discussion.—*Michaux* (1968) first named the Ailuravinae and included the European genera *Meldimys*, *Ailuravus* and *Maurimontia* (=*Ailuravus*, Wood, 1976*b*). Later, Wood (1976*b*) suggested that the North American genus *Mytonomys* should be included in this subfamily. His diagnosis for the subfamily is accepted here and does allow for the inclusion of early Eocene species of *Mytonomys* described below.

The late Eocene genus *Eohaplomys* Stock (1935) from California which has been traditionally considered an aplodontid (Wilson, 1949), has recently been shown to be more distantly related to the earliest aplodontids and is not considered an aplodontid at all (Rensberger, 1975). There is some similarity between *Eohaplomys* and late Eocene *Ailuravus* (see Wood, 1976*b*) but a complete study of both genera must be undertaken in order to determine of there is any special relationship between them.

Mytonomys Wood, 1956

Type species.—*Mytonomys robustus* (Peterson, 1919).

Range.—Early Eocene to earliest Oligocene, Wyoming, Colorado, California, Utah, and Mexico.

Included species.—*M. burkei* (Wilson, 1940), *M. coloradensis* (Wood, 1962), *M. wortmani* (Wood, 1962), and *M. gaitania* Ferrusquia and Wood, 1969.

Emended diagnosis.—Posterior margin of anterior root of zygoma level with middle of M^1; P^4 expanded buccally, nearly circular in outline with distinct conules and no hypocone; molars long with anterior cingulum widely separated from protoloph; hypocone distinct with notches present on either side of protocone lingually; mesostyle on upper molars large or multiple, extending lingually into central basin; buccal margin of M^1–M^2 convex at paracone; lower molars with broad accessory crenulations running into talonid basin; trigonid basins minute; M_3 elongate; posterolophid on lower molars distinct and separated from entoconid at least on M_2; partial hypolophid present on M_1–M_2.

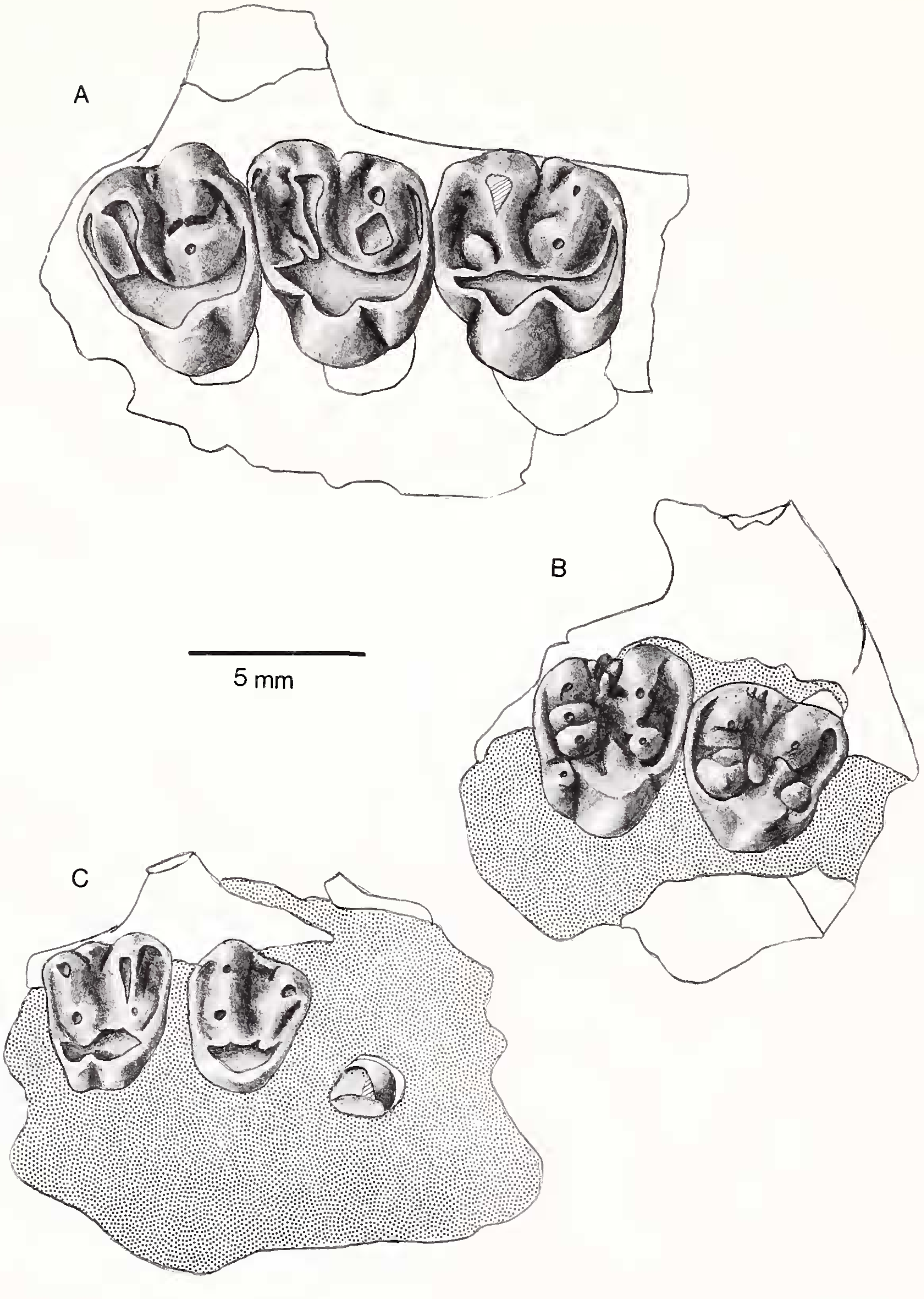


Fig. 23.—Upper dentitions of *Mytonomys.* A) *M. robustus,* LP^4–M^2. B) *M. coloradensis,* RP^4–M^1, FMNH P 26596, holotype. C) *M. wortmani,* RP^3–M^1, CM 22208.

Mytonomys coloradensis (Wood, 1962)
(Figs. 23b, 24b)

Pseudotomus coloradensis Wood, 1962.
Leptotomus loomisi Wood, 1962.

Type specimen.—FMNH P 26596, two maxillary fragments with RP^4–M^1 and LM^1–M^2.

Horizon and locality.—Type from the Lysite equivalent, Debeque Formation, Colorado. Referred specimens from the Lysite Member, Wind River Formation and from the Gray Bull, Lysite and possibly Lost Cabin levels, Willwood Formation, Wyoming.

Age.—Early, middle and possibly late early Eocene (Graybullian to ?Lostcabinian).

Referred specimens.—ACM 2568, CM 36086, ACM 335a (from Lysite Member, Wind River Formation); FMNH P 26788 (from Debeque Formation); AMNH 4966, 4968, 55946, 55948 (from Graybullian or Lysitean, Willwood Formation); and AMNH 15138 (from ?Lostcabinian, Willwood Formation).

Emended diagnosis.—Mesoconid large and crenulations present but relatively low on lower molars; metaconules on upper cheek teeth multiple; lingual notch anterior to protocone on M^2 less distinct than the posterior notch; anterior cingulum on P^4 restricted to parastylar area; P_4 nearly equal in size to M_1; I_1 relatively narrow and parallel sided.

Discussion.—Wood (1962) originally assigned *Mytonomys coloradensis* to *Pseudotomus.* However, *M. coloradensis* differs from *Pseudotomus* in having longer upper molars, more complex occlusal pattern on the molars, narrow lower incisor, more posterior position of the zygoma, lighter and more slender mandible. *Quadratomus* is the only manitshine with a lower incisor and position of the zygoma similar to those of *M. coloradensis. Quadratomus* differs from *M. coloradensis* in having broad shallow basins on all molars and a heavy mandible, lacking the irregularities of the enamel as in *Mytonomys,* and having a specialized manitshine zygoma. There are no characters of *M. coloradensis* that suggest that it is related to any manitshine.

The type of *M. coloradensis* (FMNH P 26596) is two associated maxillae with right P^4–M^1 and left M^1–M^2. The features that unite this specimen with upper dentitions of late Eocene *Mytonomys* (Black, 1968*b*) are: 1) P^4 nearly circular in outline, lacking a hypocone; 2) prominent wrinkling of enamel on the molars; 3) buccal margin of the molars convex above the paracone; 4) mesostyle complex with small lingual extension; 5) notches on the lingual margin of M^1–M^2 anterior and posterior to the protocone; and 6) posterior margin of the anterior root of the zygoma above the middle of M^1. The multiple metaconule on M^1–M^2 of *M. coloradensis* is not present on *M. robustus* from the late Eocene.

All of the lower dentitions referred by Wood (1962) to *M. coloradensis* are heavily worn and little can be determined about their occlusal morphology except that the entoconid is separated from the posterolophid on M_2. The lower incisor of *M. coloradensis* closely resembles that of *Quadratomus* except that the sides are more nearly parallel.

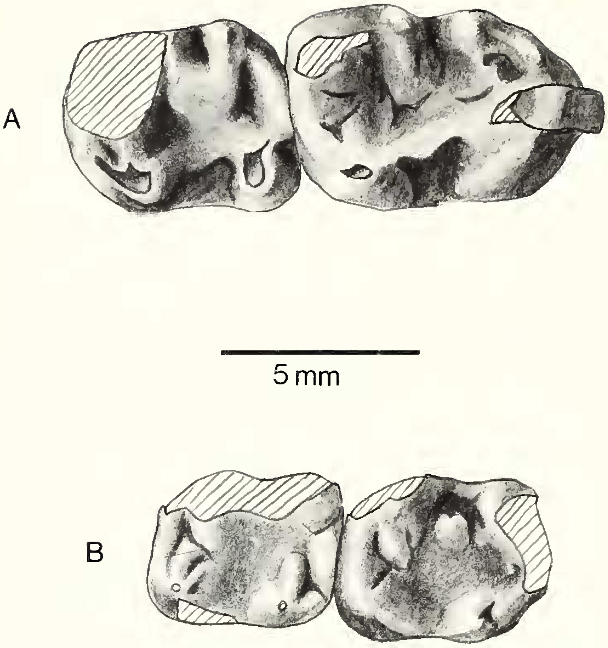


Fig. 24.—Lower dentitions of *Mytonomys.* A) *M. robustus,* LM_2–M_3, FMNH 8786. B) *M. coloradensis,* RM_2–M_3, ACM 335a (=holotype of *Leptotomus loomisi*).

The holotype of *Leptotomus loomisi* (ACM 335a) agrees in size of the molars and morphology of the lower incisor with referred specimens of *M. coloradensis.* The I_1 of *M. coloradensis* figured by Wood (1962a: Fig. 58d) has a narrow flattened area on the anterior surface. The anterior surface of I_1 of *L. loomisi* and other referred specimens of *M. coloradensis* is rounded. This is a minor variation in the morphology of the lower incisor and is also variable in species of *Paramys, Reithroparamys,* and *Acritoparamys.*

The type of *L. loomisi* agrees with late Eocene species of *Mytonomys* in having: 1) low, broad irregularities on the molars; 2) a short, low hypolophid running from the entoconid; 3) distinct buccolingually elongate hypoconulid on M_2; 4) posterolophid separated from the entoconid on M_2; and 5) M_3 elongate. The lower teeth of *M. coloradensis,* including *L. loomisi,* differ from those of late Eocene *Mytonomys* in having a P_4 approximately equal in size to M_1, more pronounced mesoconid with a weak ectolophid, and narrow I_1.

Black (1968*b*) commented that there was no separation between the posterolophid and the entoconid on the lower molars of *M. robutsus,* and that the entoconid just rose high above the level of the posterolophid. However, the entoconid is separated at least on M_2 of all species of *Mytonomys.*

Because no associated upper incisors of *M. coloradensis* have been recovered, the isolated incisors previously identified as this species from the Lost Cabin Member, Wind River Formation (Wood, 1962; Guthrie, 1971) should not be referred to this species.

Wood (1962: Tables 27, 58, 60) provided dental measurements of *Mytonomys coloradensis.*

Mytonomys wortmani (Wood, 1962)
(Fig. 23b)

Type specimen.—AMNH 4761, associated mandibles with LP_4–M_2 and RM_1–M_3 and some associated postcranial bones.

Horizon and locality.—Type and all referred specimens from type area of the Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—WAM 6001, CM 22208.

Emended diagnosis.—Smallest species of the genus; protoloph weakly developed on P^4; P_4 smaller than M_1; posterolophid separated from entoconid on P_4–M_2; accessory crenulations weakly developed on molars.

Description.—The posterior margin of the zygoma of *M. wortmani* is level with the center of M^1. The infraorbital foramen is small. Only part of the border of the infraorbital foramen is preserved on one specimen (CM 22208) so that the exact size of the infraorbital foramen cannot be determined.

P^3 is typically single rooted and peg-like. It is slightly larger relative to P^4 than is the case of *Paramys copei.* Nothing can be said about the morphology of the occlusal surface of P^3, since the only known specimen is heavily worn.

P^4 is submolariform and slightly smaller than M^1. The paracone is far anterior and lingual to the metacone which creates a broad low valley which runs buccolingually across the tooth. The paracone attaches directly to the protocone by way of a broad, short protoloph. There is no indication of a protoconule. The anterior cingulum runs about half the width of the tooth from the apex of the paracone buccally to the anterobuccal extent of the protocone. The metacone is anteroposteriorly compressed. The circular metaconule is nearly as large as the metacone. The metaloph runs anterolingually and joins the protoconid. The posterior cingulum extends the entire width of the tooth. Only a minute mesostyle is present between the metacone and paracone. There are some irregularities on the surface of the enamel.

M^1 is the only upper molar known from *M. wortmani.* The buccal border of the tooth is convex in the parastylar area. The anterior cingulum is widely separated from the paracone but runs posterolingually, joining the protocone buccal to the lingual margin of the tooth. This feature makes the tooth shorter lingually than bucally. The paracone and metacone of M^1 are subequal in size and compressed anteroposteriorly. The protoloph runs directly lingual with a distinct protoconule just buccal to the protocone. The metaloph runs anterolingually to the protocone. The metaconule is larger than the protoconule and placed lingually on the metaloph. The posterior cingulum is closely appressed to the metaloph and runs the entire width of the tooth. There is a large mesostyle which extends into the valley between the metacone and paracone. As in P^4, there are some minor irregularities on the enamel surface.

Discussion.—Wood (1962) described *Paramys wortmani* on the basis of lower dentitions and a few postcranial bones. Guthrie (1971) synonymized *P. wortmani* with *P. copei,* stating that the differences between these two species were within the bounds of variation of a species. However, it does seem that the separation of the entoconid from the posterolophid on the lower cheek teeth, slightly larger size, and wider I_1, clearly separate *M. wortmani* from *P. copei.*

A maxilla with P^3–M^1 (CM 22208) from the Lost Cabin Member, Wind River Formation is here referred to *M. wortmani* based on its slightly larger size than *P. copei* and morphology of the cheek teeth and position of the zygoma that more nearly resemble other species of *Mytonomys.*

The holotype of *M. wortmani* is very heavily worn so many features are obscured, but still there are similarities to late Eocene *Mytonomys.* Wood (1962: 37) noted that there were irregularities on the enamel of the molars but suggested that these indicated affinities with *Thisbemys.* The crenulations on M_3 of the holotype of *M. wortmani* are barely recognizable but appear to be broader than those of *Thisbemys,* more nearly approaching other species of *Mytonomys* in this feature. The separation of the entoconid on P_4–M_2 of *M. wortmani* also allies it with *Mytonomys.* There appears to be a short, low hypolophid running into the talonid basin from the entoconid of M_1–M_2 of *M. wortmani,* as in other *Mytonomys.* This feature is also obscured by wear and the original length and height of this loph cannot be determined.

The maxilla referred to *M. wortmani* differs from those of *Paramys* and is similar to other *Mytonomys* in several features: 1) posterior margin of anterior root of the zygoma level with eenter of M^1; 2) P^4 expanded anteriorly giving the tooth a more nearly circular occlusal outline; 3) M^1 elongate anteroposteriorly; 4) anterior cingulum of M^1 widely separated from protoloph; 5) buccal margin of M^1 at paracone convex; and 6) hypocone on M^1 large, creating a deep notch on the lingual margin of the tooth between it and the protocone.

M. wortmani differs from other species of *Mytonomys* in having a relatively smaller P_4 that is very narrow anteriorly, having less pronounced irregularities on the enamel of the molars, having the entoconid separated from the posterolophid on M_1, having P^4 less circular in occlusal outline, and having only a faint notch on the lingual margin of M^1 anterior to the protocone.

In all of these features, *M. wortmani* is more primitive than *M. coloradensis* and the late Eocene species of *Mytonomys*. The double metaconule on the upper molars and narrower I_1 of *M. coloradensis* remove it from an ancestral position to later species of the genus. *Mytonomys wortmani* has the primitive single metaconule on the upper molars and an I_1 that is widest anteriorly, resembling I_1 of *Paramys copei*. There are no features which would remove *M. wortmani* from representing an ancestral stock for all later *Mytonomys*.

Two specimens listed by Wood (1962: 36) in the hypodigm for *M. wortmani* (AMNH 4760b, AMNH 4760c) are referable to *P. copei*.

Family Sciuravidae Miller and Gidley, 1918

Sciuravus Marsh, 1871

Type species.—*Sciuravus nitidus* Marsh, 1871.

Sciuravus wilsoni Gazin, 1961

Type specimen.—USNM 22425, right mandible with P_4–M_2.

Horizon and locality.—Type and referred specimen from center of T29N, R91W, Sublette County, Knight Member, Wasatch Formation, Wyoming. Other referred specimens from Cathedral Bluffs Tongue, Wasatch Formation, Wyoming.

Age.—Late to latest early Eocene (Lostcabinian to Gardnerbuttean).

Referred specimens.—USNM 22424 (from Knight Member) and PU 17785 (from Cathedral Bluffs).

Discussion.—No additional specimens of *Sciuravus wilsoni* have been described since Gazin's (1961, 1962) description of the species. The isolated teeth from the Cathedral Bluffs Tongue referred to *S. wilsoni* (PU 17785, previously cited as PU 16109) consist of P_4, M_1, two M_2s, and two M_3s. An M_2 of *Knightomys depressus* is also included with these specimens. The molars included in PU 17785 are slightly larger than those of the holotype (Gazin, 1962: 50) but distinctly smaller than the original sample of the Bridgerian species *S. nitidus* reported by Wilson (1938:133). West (1973: Table 27) listed measurements for a large sample of *S. nitidus*. The size ranges listed overlapped the sizes of both *S. nitidus* and *S. wilsoni*. West, however included specimens from the Cathedral Bluffs Tongue and the Bridger Formation in his table, and may have mixed the two species of *Sciuravus* in his sample thus giving an erroneous size range for *S. nitidus*. In all other samples, *S. wilsoni* is smaller than *S. nitidus*.

Knightomys Gazin, 1961

Type species.—*Knightomys senior* (Gazin, 1952).

Range.—Early Eocene of Wyoming, Colorado, and New Mexico.

Referred species.—*K. depressus* (Loomis, 1907), *K. huerfanensis* (Wood, 1962) and *K. minor* (Wood, 1965).

Emended diagnosis.—Small sciuravids; single sagittal crest on skull; anterior zygomatic root arises anterior to P^4; masseteric fossa on mandible ends anteriorly below posterior margin of M_1; second minute mental foramen present on mandible; cheek teeth cuspate with rudimentary loph development; protoloph and metaloph complete and separate on upper molars; entoconid on lower molars isolated with incomplete hypolophid entering into talonid basin; mesoconid distinct on lower molars and extends posterolingually into the talonid basin on M_2–M_3; minute metastylid present on lower cheek teeth.

Discussion.—*Knightomys* was named by Gazin (1961) for *Tillomys senior* Gazin (1952) from the early Eocene Knight Member of the Wasatch Formation. Wood (1965) recognized that *Sciuravus depressus* Loomis (1907) from the Lysite Member of the Wind River Formation was referable to Gazin's genus and described the skull of *Knightomys*, basing this description of the holotype of *K. depressus* (ACM 432), a badly crushed partial skull. A number of Wood's observations appear incorrect based on additional skull material of *K. depressus* and *K. huerfanensis*.

The skull of *Knightomys* most closely resembles the skull of *Sciuravus* (Wood, 1965; Dawson, 1961) but is more elongate with a less inflated cranium. A low sagittal crest runs from the posterior margin of the skull and divides posterior to the orbits at the point of maximum postorbital constriction. The point of bifurcation of the sagittal crest varies on the known skulls of *Knightomys* but is generally near the same point as in *Sciuravus* (Dawson, 1961). Supraorbital ridges are developed in *Knightomys* somewhat more so than in *Sciuravus*.

The zygoma is thin and the scar on its ventral

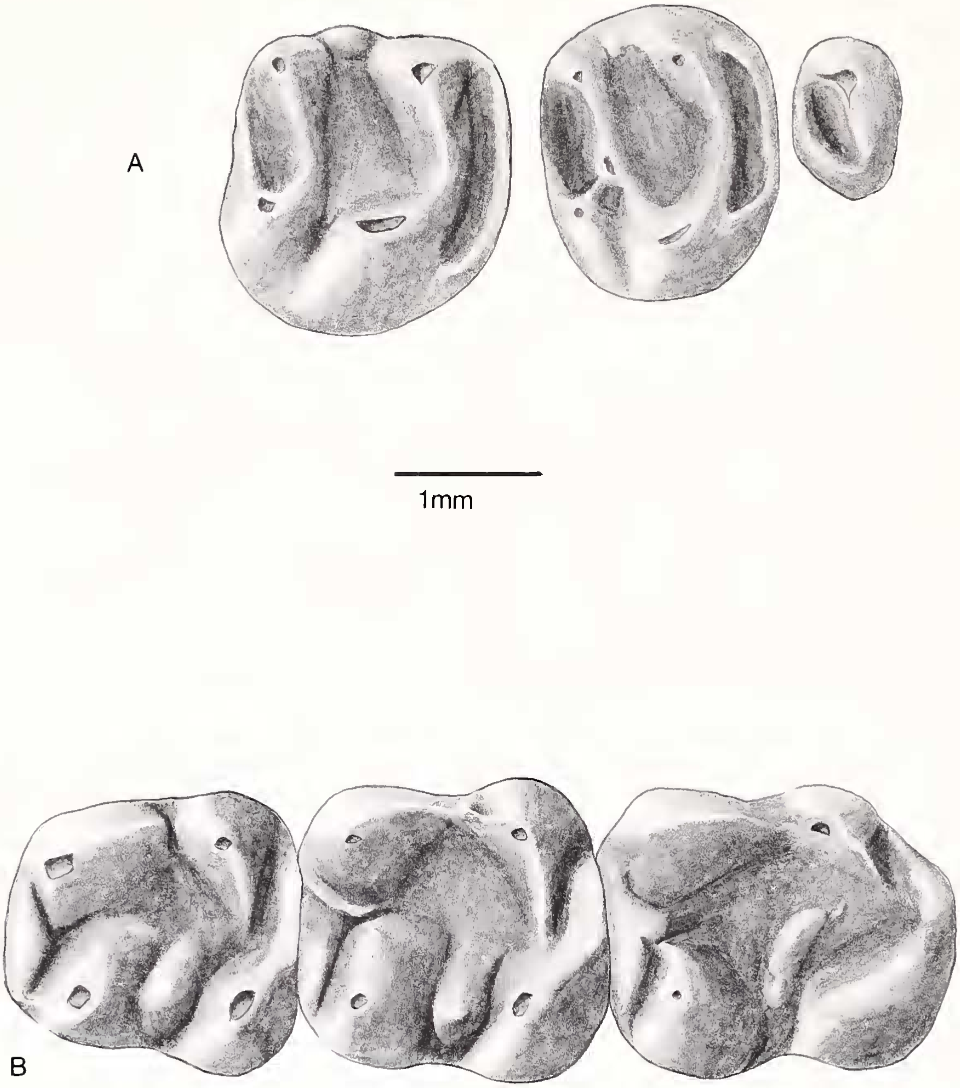


Fig. 25.—Cheek teeth of *Knightomys depressus.* A) RP^3–M^1, KU 16564. B) LM$_1$–M$_3$, CM 21155.

side for the attachment of the masseter muscle is limited to the anterior root. The posterior margin of the anterior root of the zygoma is even with the anterior margin of P^4, as in *Sciuravus* and *Microparamys.*

Contrary to Wood (1965), the infraorbital foramen of *Knightomys* (known for both *K. depressus,* AMNH 55112, and *K. huerfanensis,* CU 29944) is small. It is equal in relative size to that of *Sciuravus.* The skull on which Wood based his observations is badly damaged and the infraorbital foramen, artificially enlarged. No other foramina except the incisive foramina and foramen magnum are preserved on any of the skulls of *Knightomys.* The basicranial region is also not preserved on any of these specimens.

The pattern of sutures on the skull of *Knightomys* are virtually identical to those of *Sciuravus* (see Dawson, 1961; Wahlert, 1974). However, the present skull material of *Knightomys* does not allow determination of the presence or size of an interparietal bone. Any other specific features of the skull will be discussed under the separate species of *Knightomys.*

Knightomys depressus (Loomis, 1907)

(Fig. 25, Table 10)

Sciuravus depressus Loomis, 1907.

?*Sciuravus depressus* Loomis, Troxell, 1923.
"*Sciuravus*" *depressus* Loomis, Gazin, 1962.
Microparamys lysitensis Wood, 1962.
Microparamys cathedralis Wood, 1962.
Knightomys depressus (Loomis) Wood, 1965.

Type specimen.—ACM 432, partial skull with RM^1–M^3.

Horizon and locality.—Type and some referred specimens from the type area of the Lysite Member of the Wind River Formation, Wyoming. Other referred specimens from Lost Cabin Member, Wind River Formation, Wyoming; Lysite equivalent of Debeque Formation, Colorado; Upper Huerfano Formation (localities II and III), Colorado; Cathedral Bluffs Tongue, Wasatch Formation, Wyoming; and the Largo Member, San Jose Formation, New Mexico.

Age.—Middle to latest early Eocene (Lysitean to Gardnerbuttean).

Referred specimens.—ACM 458, 487, 2951b, 2951d, 2952, 2962, 2966, 2974, 4388, 4389, CM 21791, 22847–22849, 28741, 35937, 36091, 37089, 37093, 37094, KU 16564, AMNH 12767 from Lysite Member). CM 21151–21155, 21160, 21162, 22244–22248, 22250–22252, 22254, 26503, 26514–26518, 29153–29157, 29159, 29164, 35860–35862, 36517–36522, 36524, 36525, 36528–36530, 36920–36922, 37253, 37254, CU 44359, 44368, 44706, 44715, 44837, 44841, 44845, 45218, 45221, 45225, 45328, 45358, 45068, 42825, 42857, PU 17252 (from Lost Cabin Member). FMNH PM 1226, P 26587 (from Debeque Formation). AMNH 55112, 55142, 55144, 55194, 55988, YPM 16473, CU 2148, CU 26542, 32752, 32785, 33276, 29944 (from Upper Huerfano, localities II and III). YPM 16512 (from Largo Member). PU 16112, FMNH PM 15895 (from Cathedral Bluffs Tongue).

Table 10.—*Dental measurements of* Knightomys depressus *(in millimeters).*

Measurements		N	M	S	V	OR
P_4–M_3		5	7.75	.23	2.9	7.39–7.97
P_4	a–p	18	1.69	.09	5.3	1.56–1.88
	tra	15	1.27	.09	7.1	1.11–1.42
	trp	16	1.49	.10	6.8	1.35–1.69
M_1	a–p	41	1.82	.08	4.4	1.67–2.00
	tra	37	1.51	.09	6.1	1.33–1.63
	trp	39	1.70	.10	6.2	1.44–1.89
M_2	a–p	43	1.88	.08	4.2	1.70–2.02
	tra	39	1.73	.08	4.8	1.59–1.92
	trp	41	1.84	.09	4.7	1.72–1.98
I_1	a–p	10	2.18	.20	9.3	1.70–2.49
	tra	10	1.28	.10	8.2	1.14–1.43
P^3	a–p	4	0.70	—	—	0.55–0.78
	tra	4	0.78	—	—	0.52–0.95
P^4	a–p	8	1.49	.12	8.4	1.31–1.68
	tra	8	1.73	.14	8.4	1.52–1.91
	trp	8	1.66	.15	9.1	1.43–1.90
M^1	a–p	10	1.72	.07	4.1	1.60–1.81
	tra	10	1.88	.11	5.7	1.72–2.08
	trp	10	1.78	.11	6.1	1.66–1.99
M^2	a–p	14	1.82	.12	6.8	1.57–2.03
	tra	14	2.00	.14	7.0	1.69–2.22
	trp	14	1.82	.12	6.8	1.59–2.01
M^3	a–p	2	1.80	—	—	1.66–1.93
	tra	3	1.81	—	—	1.74–1.93
I^1	a–p	2	2.68	—	—	2.26–3.10
	tra	2	1.43	—	—	1.26–1.59

Emended diagnosis.—Intermediate sized member of the genus; anterior cingulum separated from protoconid and metaconid on unworn lower molars; hypolophid variable in length and disappears rapidly with moderate wear on lower molars; P^4 with hypocone minute; posterolingual lophid of mesoconid of M_3 very broad, extending to posterolophid.

Discussion.—The only tooth of *Knightomys depressus* not previously described is P^4. This tooth is small relative to M^1, has a complete protoloph and metaloph, which converge anteriorly at the protocone. There is no trace of a protoconule on the protoloph, but a distinct metaconule is present. Both anterior and posterior cingula run the entire width of the tooth. The hypocone is variable in size and always present. There is no mesotyle on P^4.

Knightomys depressus differs from all other species of the genus in its size. It differs from *K. minor* and *K. senior* in having separation of the anterior cingulum from the protoconid on the lower molars and the minor swelling of the anterior cingulum buccally.

Contrary to Wood's (1965) observations, the metaconule on the upper molars is not connected to the protocone and hypocone by lophs of equal height. Only in the holotype (ACM 432) is there any connection between the protocone and metaconule, and on this specimen it occurs only on M^2 via an extremely weak loph. This connection is an artifact of very heavy wear of the tooth of the holotype, and the metaconule wear facet has merged with the facet of the protocone. Gazin's (1962: Pl. 5, Fig. 8) figure of this specimen clearly shows the separation of the protoloph from the metaloph.

Guthrie (1971) referred two of Wood's (1962) species, *Microparamys lysitensis* and *M. cathedralis*, to *K. depressus* because the only differences separating these species from *K. depressus* was the stage

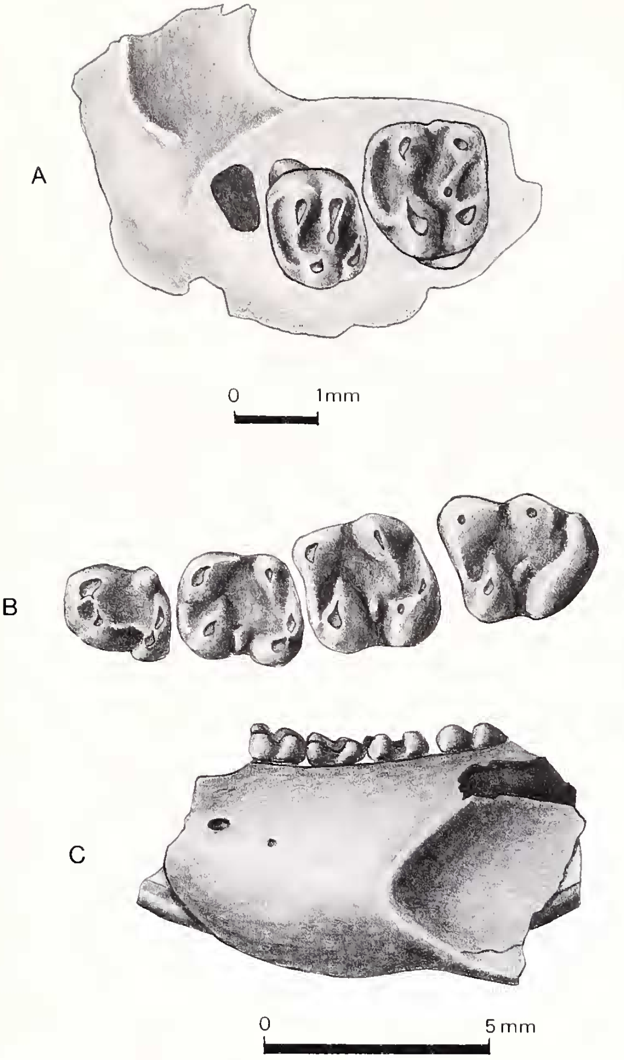


Fig. 26.—Associated upper and lower cheek teeth of *Knightomys minor*, CM 36090. A) LP^4–M^1. B) LP_4–M_3. C) Lateral view of mandible.

of wear of the tooth. Wood (1962: Fig. 54o) noted the unique shape of I_1 of *M. cathedralis* as a specific character. However, I_1 of the type of *M. cathedralis* is much more parallel sided than figured by Wood, and does not differ from that of *K. depressus.*

Knightomys depressus is the most common sciuravid in the early Eocene. No differences in size or morphology can be found between specimens of *K. depressus* from its earliest occurrence (Lysitean) through its latest (Gardnerbuttean).

Knightomys minor (Wood, 1965)
(Fig. 26, Table 11)

Dawsonomys minor Wood, 1965.

Type specimen.—ACM 4387, left mandible with P_4–M_3.

Horizon and locality.—Type and some referred specimens from the type area of the Lysite Member, Wind River Formation, Wyoming. Other referred specimens from Lysite equivalent Debeque Formation, Colorado.

Age.—Middle early Eocene (Lysitean).

Referred specimens.—CM 35927, 36089, 36090, 37095–37097, PU 17257 (from Lysite Member). FMNH PM 1229, PM 1223, P 26502 (from Debeque Formation).

Emended diagnosis.—Smallest species of genus; anterior cingulum on the lower molars narrow and connected to the protoconid and metaconid; small cuspule present in center of anterior cingulum on M_1; no anterior cingulum on P_4.

Discussion.—Wood (1965) named *Dawsonomys minor* from the Lysite beds of the Wind River Formation on the basis of a mandible with P_4–M_3. He referred his new species to *Dawsonomys* because of the nearly complete hypolophid on the molars. Additional specimens of this species, including associated upper and lower dentitions, show that this species is referable to *Knightomys.*

Knightomys minor differs from *Dawsonomys* in having: 1) less lophate teeth; 2) hypolophid on molars weak and variable in length; 3) trigonid of the lower molars not compressed or elevated; 4) large distinct mesoconid on M_1–M_3; 5) narrower I_1; and 6) a doubled mental foramen on the mandible. The lower teeth of *K. minor* resemble those of other species of *Knightomys* in all these features. The degree of loph development in *K. minor* is equal to that in *K. senior* and *K. depressus.* The mesoconid on M_2 and M_3 has a loph arising from it which runs posterolingually into the talonid basin, also as in other species of *Knightomys.* The upper molar of *K. minor* does not differ from those of *K. depressus* except in being smaller. The hypocone on P^4 is relatively large in *K. minor,* equivalent to the size of the hypocone on P^4 of *K. depressus.*

Knightomys minor is distinguishable from all other species of the genus by its smaller size and attachment of the anterior cingulum to the protoconid on the lower molars. A specimen from the type area of *K. minor* (CM 36091) consists of the anterior portion of the rostrum with both upper incisors, which are of appropriate size to be assigned to *K. minor* and have a similar cross-sectional shape to those in *K. depressus* (see Wood, 1965: Text-fig. 2e). The unique feature of this specimen is that the left

Table 11.—*Dental measurements of* Knightomys minor *(in millimeters).*

		CM 37096	CM 36090	CM 36089	CM 37097	CM 37095	ACM 4387*	FMNH P26502	CM 36090	FMNH PM 1229	FMNH PM 1223
P_4	a–p	1.32	1.26				1.18	1.30			
	tra	1.09	0.91				0.98	1.00			
	trp	1.23	1.10				1.15	1.10			
M_1	a–p	1.31	1.50	1.42			1.44	1.39			
	tra	1.12	1.23	1.22			1.17	1.19			
	trp	1.23	1.33	1.39			1.33	1.34			
M_2	a–p		1.54	1.54	1.61	1.45	1.40	1.49			
	tra		1.41	1.41	1.45	1.44	1.34	1.47			
	trp		1.46	1.47	1.51	1.49	1.38	1.59			
M_3	a–p		1.74				1.67	1.59			
	tra		1.44				1.39	1.45			
	trp		1.39				1.30	1.33			
P_4–M_3			6.16				5.70	6.05			
P^4	a–p								1.19		
	tra								1.40		
	trp								1.29		
M^1	a–p								1.43	1.41	1.31
	tra								1.60	1.65	1.43
	trp								1.45	1.59	1.33

* Taken from Wood (1965: Table 3).

incisor is rounded and smooth anteriorly, as in *K. depressus,* but the right I^1 has a minute groove that runs the entire length of the tooth. This groove is not broad and shallow, a feature relatively common on I_1 of many ischyromyids but is very narrow.

Knightomys senior (Gazin, 1952)
(Fig. 27, Table 12)

Tillomys senior Gazin, 1952.
Knightomys senior (Gazin) Gazin, 1961.

Type specimen.—USNM 19308, right mandible with P_4–M_2.

Horizon and locality.—Type from LaBarge (Gazin, 1952:6), Knight Member, Wasatch Formation, Wyoming. Referred specimens from the Lost Cabin Member, Wind River Formation, Wyoming; and possibly the Almagre Member, San Jose Formation, New Mexico.

Age.—Late and possibly middle early Eocene (Lostcabinian and possibly Lysitean).

Referred specimens.—USNM 22415 (from Knight Member). CU 42823, 44703, 44718, 44839, 44844, 45253, 45277, 45327, CM 38736 (from Lost Cabin Member). Possibly AMNH 48165–48167, 48169, 48170 (from Almagre Member).

Emended diagnosis.—Smaller than *K. depressus* and larger than *K. minor*; anterior cingulum on the

Table 12.—*Dental measurements of* Knightomys senior *(in millimters).*

Specimen nos.	M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
CU 45277	1.70	1.31	1.55						
CU 45253	1.74	1.39	1.51						
CM 38736				1.65	1.55	1.66	1.93	1.57	1.55
CU 42823							1.95	1.66	1.59
	M^1			M^2			M^3		
CU 45327	1.54	1.54	1.48						
CU 44703				1.61	1.60	1.55			
CU 44844							1.69	1.72	—

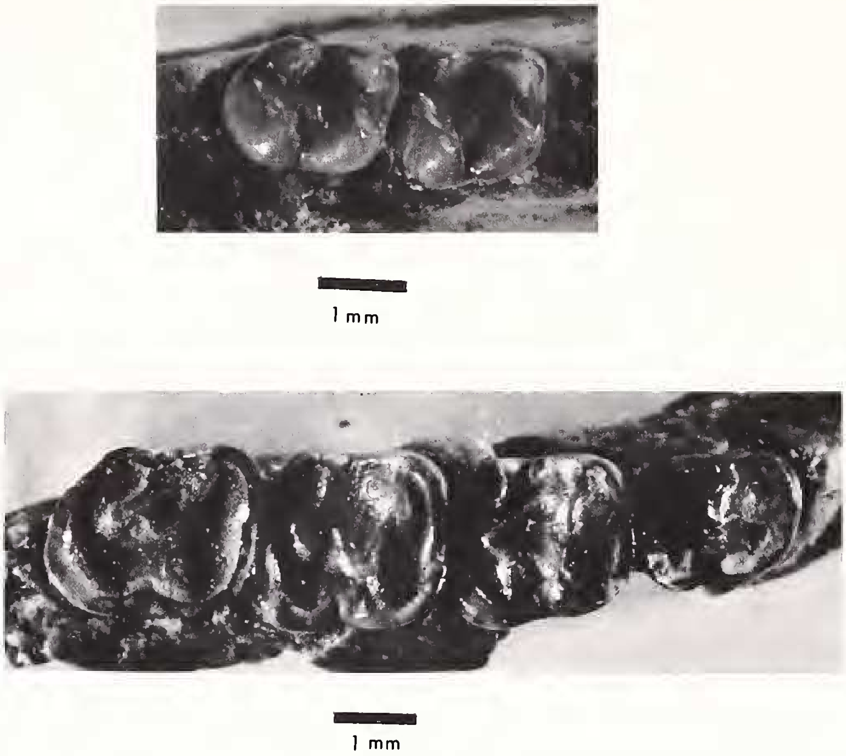


Fig. 27.—Lower dentitions of *Knightomys senior* and *K. huerfanensis*. A) *K. senior*, RM$_2$–M$_3$, CM 38736. B) *K. huerfanensis*, RP$_4$–M$_3$, AMNH 55114, holotype.

lower molars connected to protoconid; mesoconid on M$_2$–M$_3$ less elongated; hypolophid on lower molars short.

Discussion.—Gazin's (1952, 1961, 1962) hypodigm of *Knightomys senior* consisted of three mandibles, all with very heavily worn cheek teeth. Several specimens from San Jose Formation are questionably referable to this species. The specimens from New Mexico are slightly smaller than *K. senior* and slightly larger than *K. minor*. The specimens of *K. senior* from the Lost Cabin Member of the Wind River Formation are equivalent in size to the typotypic material of *K. senior* and are less worn, thus helping to define the species.

Wood (1965) separated *K. senior* from *K. depressus* on only a few distinctions: 1) single mental foramen in *K. senior*, double in *K. depressus*; 2) hypolophid on the molars of *K. senior* is directed toward the hypoconulid; 3) sides of I$_1$ of *K. depressus* are more nearly parallel; and 4) *K. senior* is smaller.

The first distinction, a single mental foramen on *K. senior*, is incorrect. The type of *K. senior* and all referred specimens of the species have a minute second mental foramen as in all other *Knightomys* (see Gazin, 1962: Pl. 5, Fig. 6). The second difference, the direction of the hypolophid, is variable in *K. depressus* and could not be determined from the specimens in Gazin's (1962) hypodigm. The new material of *K. senior* shows that the hypolophid on the molars is very short and less variable in length and direction than in *K. depressus*. There is no real distinction between the lower incisors of *K. depressus* and *K. senior* except for size.

In all, size is the only difference between *K. depressus* and the original hypodigm of *K. senior*. The specimens from the Lost Cabin Member of the Wind River Formation preserve better the occlusal morphology of the cheek teeth of *K. senior*. These specimens differ from *K. depressus* in having: 1) a thin anterior cingulum connecting with the protocone as in *K. minor*; 2) an entoconid with a shorter hypolophid; and 3) a smaller mesoconid that does not extend as far into the talonid basin. These differences, along with smaller size, distinguish *K. senior* from *K. depressus*. *Knightomys senior* is larger than *K. minor*, and does not possess the central cuspule on the anterior cingulum of M$_1$ of *K. minor*.

The single specimen from the Cathedral Bluffs

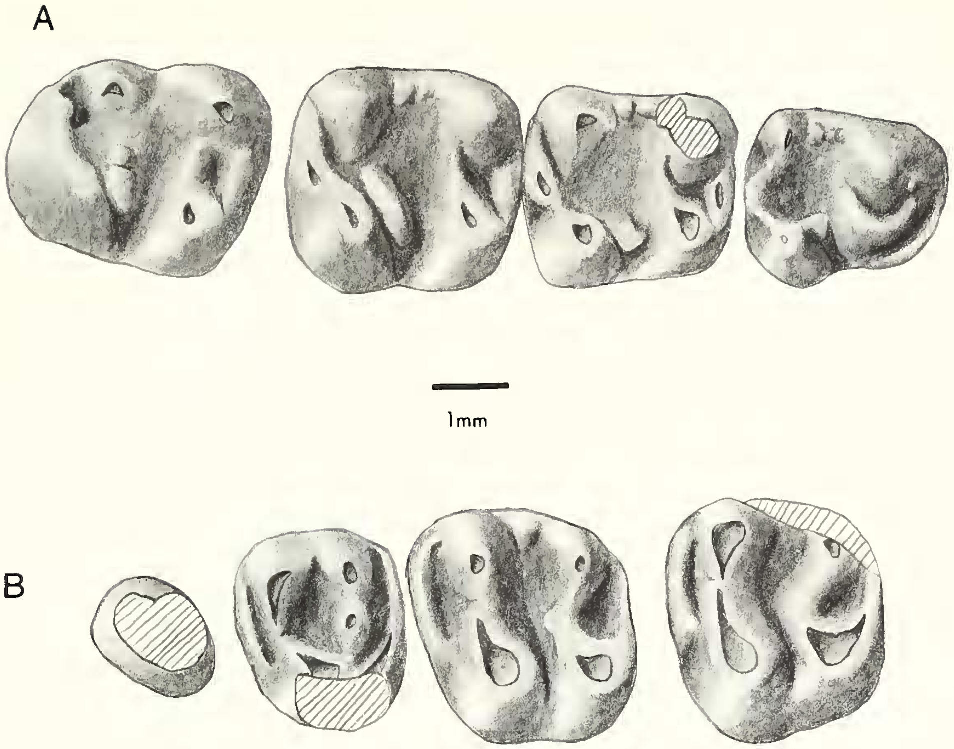


Fig. 28.—Cheek teeth of *Knightomys huerfanensis.* A) RP$_4$–M$_3$, AMNH 56523. B) LP^3–M^2, CU 26233.

Tongue of the Wasatch Formation allocated by West (1973) to *Knightomys* cf. *K. senior* is here referred to *K. depressus.*

Knightomys huerfanensis (Wood, 1962)
(Figs. 27, 28, Table 13)

Paramys huerfanensis Wood, 1962.
Microparamys sp. B Wood, 1962.
Knightomys sp. West, 1973.

Type specimen.—AMNH 55114, right mandible with worn P$_4$–M$_3$.

Horizon and locality.—Type and some referred specimens from localities II, III, V, upper Huerfano Formation, Colorado. Other referred specimens from Cathedral Bluffs Tongue, Wasatch Formation, Colorado; and Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late to latest early Eocene (Lostcabinian to Gardnerbuttean).

Referred specimens.—AMNH 17025, 17462, 55115, 55119, 55131, 55136, 55140, 55191, 55200, 55989, 56523, YPM 16438, 16480, CM 19537, CU 22040, 26233, 29944, 32753, 32786, 33267, 33272 (from Upper Huerfano, localities II, III, V). FMNH PM 15524, PM 15587, PM 15889 (from the Cathedral Bluffs Tongue). CM 37175, CU 42852, 42854, 44723, 45224, 45420 (from Lost Cabin Member).

Emended diagnosis.—Largest species of genus; cusps on cheek teeth large and rounded; hypolophid on lower molars short; lophs on molars relatively high; metaloph and protoloph on P^4 nearly parallel; anterior cingulum separated from protoconid and metaconid on lower molars.

Description.—*Knightomys huerfanensis* is distinctly larger than any other species of *Knightomys.* The skull and mandible of *K. huerfanensis* strongly resemble those of *K. depressus* but are larger and more robust. Little else can be determined from the skull material of *K. huerfanensis* because of its poor condition (CU 29944).

The cusps on the cheek teeth of *K. huerfanensis* are large and high. The lophs on the cheek teeth are also higher than in any other species of *Knightomys.*

P^4 has a relatively large hypocone. The metaloph and protoloph converge at the protocone but are more nearly parallel than in other species. There is no protoconule but the metaconule is distinct.

The upper molars differ from those of other species only in having higher, more rotund cusps. In other species of *Knightomys,* the protocone and hypocone of M^1–M^2 are more cresentic. In *K. huerfanensis,* these cusps are more nearly circular. The upper incisors of *K. huerfanensis* differ from those of *K. depressus* only in being larger.

As in the upper molars, the lower cheek teeth of *K. huerfanensis* are distinct from other species in having higher cusps and lophs. The anterior cingulum on the molars is reduced to a globular

Table 13.—*Dental measurements of* Knightomys huerfanensis *(in millimeters).*

Specimen nos.	P_4			M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
AMNH 55989	—	—	—	2.10	1.79	1.95	—	—	—	—	—	—
AMNH 17462	—	—	—	—	—	2.09	2.23	1.97	2.18	2.55	2.05	2.1
YPM 16480	—	—	—	—	—	—	—	—	—	2.25	1.99	1.6
AMNH 55119 L	2.06	1.66	1.79	2.17	1.88	2.08	2.40	2.12	2.09	—	—	—
AMNH 55119 R	2.13	1.53	1.74	2.10	1.88	2.04	2.36	2.04	1.99	2.73	2.09	2.0
AMNH 55191	2.07	1.52	1.78	2.16	—	—	2.25	2.14	2.35	2.56	2.10	2.1
AMNH 55136	2.04	1.47	1.73	2.07	1.75	1.89	2.12	1.98	2.07	—	—	—
AMNH 55131	—	—	—	—	—	—	2.19	2.05	2.10	2.47	1.96	2.0
AMNH 55140	—	—	—	2.06	1.64	1.89	2.15	1.88	2.10	—	—	—
AMNH 56523	2.00	1.53	1.74	2.14	1.79	1.97	2.20	2.11	2.08	2.50	2.00	1.8
CU 32753	1.86	1.38	1.62	2.12	1.69	1.85	2.23	1.86	2.02	2.32	1.87	1.9
CU 29944	—	—	—	2.02	—	1.98	—	—	—	—	—	—
	P^4			M^1			M^2			M^3		
CU 26233 L	1.73	1.98	2.06	2.17	2.34	2.23	2.14	2.46	2.21	—	—	
CU 26233 R	—	—	—	—	—	—	2.11	2.51	2.19	1.96	2.27	
CU 32786	1.92	2.20	2.04	—	—	—	—	—	—	—	—	
CU 19537	1.64	2.09	1.98	—	—	—	—	—	—	—	—	
CU 22040	—	—	—	—	—	—	2.08	2.22	2.07	2.13	2.17	
CU 33267	—	—	—	2.21	2.44	2.25	—	—	—	—	—	
CU 33272	1.87	2.23	2.10	—	—	—	—	—	—	—	—	

swelling along the anterior margin of the tooth. It is not connected to any cusp. The metastylid on all the lower cheek teeth is larger and more distinct than in any other species of the genus. The hypolophid on the lower molars is short and directed buccally. It is shorter than in many specimens of *K. depressus* or *K. minor*, but is high and persists until late stages of wear.

The lower incisor of *K. huerfanensis* is narrow and parallel sided, resembling that of all other species of the genus. The anterior surface of I_1 is either flattened or convex.

Discussion.—The holotype of *Knightomys huerfanensis* (AMNH 55114) is a mandible with heavily worn cheek teeth. Because the occlusal pattern of the cheek teeth of the type is so badly obscured, Wood (1962) could not distinguish any of the sciuravid characters of the species, and referred it to *Paramys*. Additional unworn specimens from the Huerfano, the type area of the species, indicate that this species is readily assignable to *Knightomys*. *Knightomys huerfanensis* differs from *K. depressus* only in its larger size and more robust cusps and lophs on the cheek teeth.

Wood (1962) identified a single specimen from the Huerfano as an upper molar of *Microparamys* sp. B (AMNH 55200). This tooth agrees in size and morphology with P^4 of *K. huerfanensis*.

Three isolated molars from the Cathedral Bluffs, originally identified as *Knightomys* sp. (West, 1973), are also referable to *K. huerfanensis*.

Pauromys Troxell, 1923

Type species.—*Pauromys perditus* Troxell, 1923.

Pauromys sp.
(Fig. 29, Table 14)

Referred specimens.—CU 44710, 44711, 44713, 44734, 44842, 45258, 45259, 45270, 45292.

Horizon and locality.—Deadman Butte area (Stucky and Krishtalka, 1982), Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Description.—The upper molars are square in outline. The protoloph and metaloph are distinct buccolingually directed lophs. The anterior cingulum runs parallel to the protoloph from the buccal margin of the tooth to the level of the apex of the protocone. The posterior cingulum arises from the hypocone and runs the entire width of the tooth. No protoconule is present. A minute anterior projection originates at the metaconule and runs about half the width of the valley separating the protoloph and metaloph. A second minor loph originates from the protocone and runs posterobuccally toward the metaconule spur but does not connect with it on unworn specimens. A minute mesostyle is present. A single dP^4 (CU 44373), near the size of the upper molars of *Pauromys* sp., may represent this species. This tooth is triangular in occlusal outline, the hypocone is posterobuccal to the protocone and separated from the protoconid. The posterior cingulum, originating at the hypocone, runs the width of the tooth. The protocone is connected to the buccal cusps (paracone and metacone) by the protoloph and metaloph which converge on the protocone.

P_4 is quite small and triangular in shape. The metaconid dominates the trigonid with a small, closely appressed protoconid. The mesoconid is minute and isolated. The entoconid and hypoconid are connected by a continuous posterolophid.

M_1 is narrower anteriorly than posteriorly. The anterior cin-

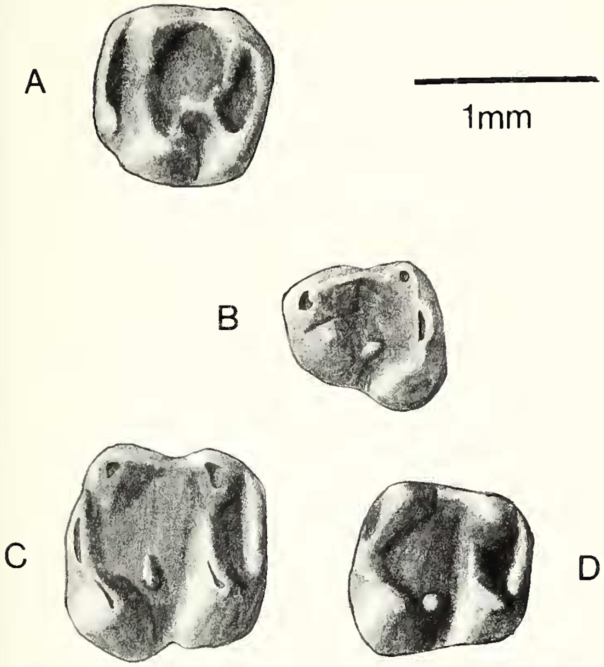


Fig. 29.—Cheek teeth of *Pauromys* sp. A) LM^1 or M^2, CU 44710. B) LP_4, CU 45270. C) RM_2, CU 45292. D) RM_1, CU 44713.

gulum is short but extends anterior of the protoconid and metaconid, not continuous with either cusp. The posterior arm of the protoconid is relatively long, ending lingually at the posterobuccal corner of the metaconid. A small, low ridge from the metaconid enters the trigonid basin. A metastylid is present on the posterolingual slope of the metaconid. The mesoconid, as in P_4, is minute and isolated. The hypoconid is connected to the entoconid by way of the posterolophid which flexes at its center.

M_2 is nearly square in outline. The anterior cingulum and posterior arm of the protoconid are arranged as in M_1. The mesoconid is isolated but extends lingually into the talonid basin. The hypoconid is continuous with the posteroloph but separated from the entoconid. A low partial hypolophid runs buccally from the entoconid.

Discussion.—All specimens of *Pauromys* sp. from the Lost Cabin Member are isolated teeth. The molars assigned to this species are equal in size to the molars of *Pauromys perditus* and *Pauromys* sp. from the Bridgerian (Troxell, 1923; Dawson, 1968*b*). The P_4 of the Lost Cabin species is larger than any P_4 of the Bridgerian species. This condition would be predicted in the earlier species if reduction of the lower premolar is occurring in this genus through time.

The molars of the Lost Cabin species have lower lophs than the Bridgerian species but have little else that separates them from the later species. Dawson (1968*b*) noted that the minute loph from the metaconule and protocone on the upper molars of Bridgerian *Pauromys* sp. were connected on some specimens but that this was a variable character. These two small lophs never meet on the upper molars of the Lost Cabin species except when they are extremely worn.

Fig. 30.—Upper cheek tooth of an indeterminate sciuravid, AMNH 59632.

The material of *Pauromys* sp. from the Lost Cabin Member is too scanty and too similar to the Bridgerian species of *Pauromys* to establish a new species, but does confirm the trend in the reduction of P_4 and the increase in the height of the lophs in this genus through time.

?Sciuravid indeterminate

(Fig. 30)

Specimen.—AMNH 59632, isolated upper cheek tooth.

Horizon and locality.—East Alheit Pocket Quarry (McKenna, 1960), Wasatch Formation, Colorado.

Age.—Early early Eocene (Graybullian).

Description.—AMNH 59632 is a minute tooth (a–p = 1.02 mm, tra = 1.04 mm). It is approximately triangular in outline. The anterior cingulum is widely separated from the paracone but converges with the protoloph at the level of the apex of the protocone. Protoloph and metaloph converge at the protocone. Both conules are relatively large. The protoloph is not continuous between the paracone and the protoconule. The metacone is anteroposteriorly compressed and smaller than the paracone. A mesostyle is present. A hypocone nearly equal in size to the protocone is posterior and lingual to the protocone. A short loph connects it with the metaconule. The posterior cingulum originates at the hypocone and runs buccally to the level of the metacone.

Discussion.—AMNH 59632 is referred to the Sciuravidae because of the large hypocone and degree

Table 14.—*Dental measurements of* Pauromys *sp. (in millimeters).*

Measurements		CU 45270	CU 44713	CU 45292	CU 44842	CU 44710	CU 45259	CU 44711	CU 45258
P_4	a–p	0.81							
	tra	0.59							
	trp	0.73							
M_1	a–p		0.95						
	tra		0.74						
	trp		0.82						
M_2	a–p			1.07					
	tra			0.97					
	trp			1.06					
M^1	a–p				0.98	0.95	1.04	1.13	1.00
or	tra				1.08	0.94	1.08	1.13	0.96
M^2	trp				0.96	0.91	—	0.96	0.89

of loph development. It is difficult to determine exactly which tooth this specimen is. It would be difficult to call AMNH 59632 a P^4 because of its marked molariformity. However, dP^4 in most ischyromyids has a hypocone that is relatively large and lingual to the protocone and a triangular shape.

The only sciuravid or ischyromyid known from the Four Mile fauna near the size of AMNH 56932 is *Apatosciuravus bifax.* AMNH 56932 may represent a dP^4 of this species but appears too small even for *A. bifax.* The occurrence of AMNH 59632 is important because if it represents a distinct species of sciuravid, it would represent the earliest occurrence of this family.

Family ?Cylindrodontidae Miller and Gidley, 1918

Dawsonomys Gazin, 1961

Type species.—Dawsonomys woodi Gazin, 1961.

Dawsonomys woodi Gazin, 1961

(Fig. 31)

Type specimen.—USNM 19309, left mandible with P_4–M_1.

Horizon and locality.—LaBarge (Gazin, 1952:6), Knight Member, Wasatch Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Discussion.—Gazin (1961) erected *Dawsonomys woodi* based on a mandible with I_1 and P_4–M_1. He referred this genus to the Sciuravidae because of the level of development of the lophs on the cheek teeth.

Later, Wood (1965) named a second species, *D. minor,* from the Lysite Member, Wind River Formation. As mentioned above, new material of *D. minor* indicates that this species is referable to *Knightomys,* leaving only the type species in *Dawsonomys.*

No new material of *D. woodi* has been collected since Gazin's (1961, 1962) original description of the type specimen. *Dawsonomys* is here referred questionably to the Cylindrodontidae based on its similarity to the Bridgerian cylindrodontid *Mysops.* I_1 of *D. woodi* is rounded anteriorly and laterally and much broader than in sciuravids, but typical for *Mysops* and later cylindrodontids. I_1 of *D. woodi* more closely approaches that of later cylindrodontids than does that of *Mysops.* M_1 of *D. woodi* has features that agree with *Mysops* and other cylindrodontids as well: 1) anteroposteriorly compressed and elevated trigonid; 2) entoconid more anterior with a deep valley between it and the posterolophid; 3) minute mesoconid; 4) ectolophid joins hypoconid but not protoconid; and 5) a complete hypolophid.

P_4 of *D. woodi* is submolariform and has many of the features of M_1 such as a partial hypolophid and weak ectolophid. It is nearly equal in size to M_1. In *Mysops,* P_4 is reduced in size and complexity, unlike that of *Dawsonomys.*

Both P_4 and M_1 of *D. woodi* are more rectangular in outline than in *Mysops.* In all observable features, *Dawsonomys* represents a very primitive cylindrodontid. Its definite inclusion in the Cylindrodontidae should be based on additional material, especially upper cheek teeth. Based on the presently known material, *Dawsonomys* is best placed in the Cylindrodontidae, thus extending the range of the family into the early Eocene.

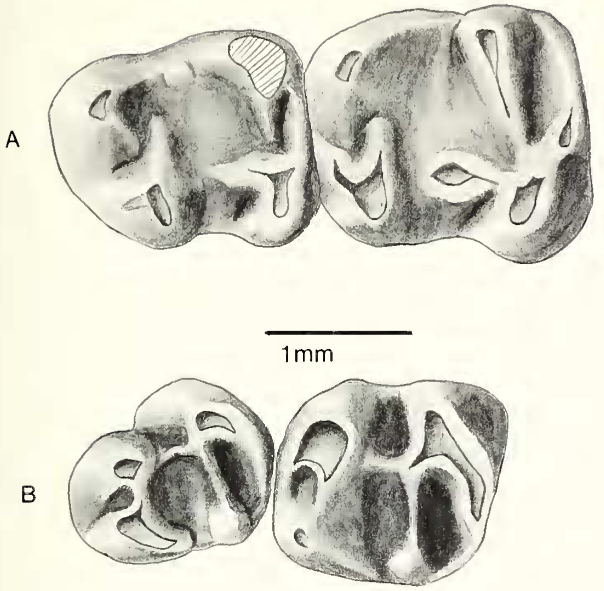


Fig. 31.—P_4–M_1 of *Dawsonomys* and *Mysops*. A) *Dawsonomys woodi*, LP_4–M_1, USNM 19309, holotype. B) *Mysops parvus*, RP_4–M_1, USNM 17663.

Family ?Eutypomyidae Miller and Gidley, 1918

Mattimys, new genus

Type species.—Mattimys kalicola (Matthew, 1918).

Range.—Early Eocene of Wyoming.

Emended diagnosis.—Very small rodent; lower cheek teeth increase in size from P_4–M_2; broad, low swellings present in talonid basin of all lower cheek teeth; mesoconids on lower molars large but ectolophids lacking; posterior arm of protoconid runs the entire width of molars, joining metaconid; anterior cingulum on molars runs entire width of tooth, extending lingually anterior to metaconid and terminating buccally as a cuspule anterior to protoconid; metaconid equal to entoconid in size; hypolophid originates from entoconid on M_1–M_2 and unites with center of posterolophid on M_1 and with hypoconid on M_2.

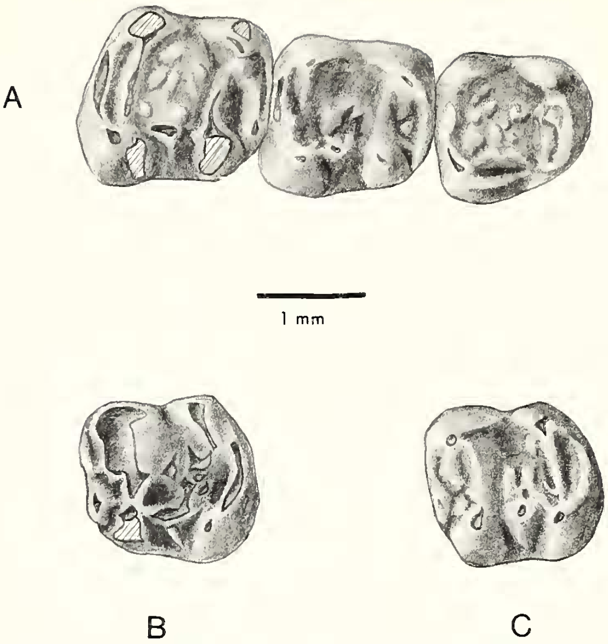


Fig. 32.—Lower cheek teeth of *Mattimys kalicola*. A) RP_4–M_2, AMNH 14731, holotype. B) LM_1, CM 36527. C) LM_2, CM 36526.

Etymology.—Patronym for W. D. Matthew, who first described *Mysops kalicola*.

Mattimys kalicola (Matthew, 1918)
(Fig. 32, Table 15)

Mysops kalicola Matthew 1918.
"*Mysops*" *kalicola* Matthew, Wilson, 1937.

Type specimen.—AMNH 14731, right mandible with P_4–M_2.

Table 15.—*Dental measurements of* Mattimys kalicola *(in millimeters).*

Specimen nos.	P_4			M_1			M_2		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
AMNH 14731	1.35	1.12	1.35	1.46	1.26	1.44	1.59	1.48	1.53
CM 22242				1.42	1.32	1.43			
CM 36523				1.45	1.36	1.39			
CM 22243				1.44	1.33	1.44			
CM 35863				1.44	1.42	1.46			
CM 36527				1.49	1.21	1.38			
CU 44365				1.49	1.24	1.36			
CM 36526							1.37	1.29	1.30
CU 44836							1.42	1.38	1.44

Horizon and locality.—Type from type area of the Lost Cabin Member, Wind River Formation, Wyoming, and all referred specimens also from the Lost Cabin Member, Wind River Formation.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—AMNH 14730, CM 22242, 22243, 35863, 36523, 36526, 36527, CU 44365, 44714, 44836, 45352.

Emended diagnosis.—As for genus.

Description.—The upper cheek teeth of *Mattimys kalicola* are not known. The mandible is shallow. The masseteric fossa on the mandible ends anteriorly below the anterior end of M_2. A single mental foramen is present on the mandible, level with the middle of the diastema anteriorly, and placed relatively high.

All of the lower cheek teeth have shallow talonid basins filled with small, randomly placed swellings that persist throughout all stages of wear. P_4 is the smallest tooth. It is rounded anteriorly. The metaconid is the largest cusp on P_4 but is not much higher than the entoconid or hypoconid. There is no mesoconid, but a low ectolophid connects the entoconid and hypoconid. There is a distinct hypoconulid at the center of the posterolophid. The anterior cingulum on M_1–M_3 runs the entire width of the tooth. It arises lingually from the anterolingual slope of the metaconid and runs anterior to the metaconid. It terminates as a small cuspule buccally anterior to the protoconid. The posterior arm of the protoconid on the molars is a relatively high loph which runs straight lingually and joins the metaconid at its base. An accessory loph runs into the trigonid basin from the metaconid and ends at the center of the basin. Another short loph into the trigonid basin from the protoconid is variably present. There is no ectolophid on the lower molars. The mesoconid is relatively large and generally has a minor loph running into the talonid basin. The posterolophid is continuous between hypoconid and entoconid. The metaconid is nearly equal in size to the entoconid, unlike early ischyromyids where the metaconid is always higher. There is no trace of a metastylid on any of the cheek teeth.

M_1 is smaller than M_2. A hypolophid runs from the entoconid on M_1 buccally and merges with the center of the posterolophid. On M_2 the hypolophid runs the entire width of the tooth and joins the hypoconid. M_3 is rounded posteriorly and lacks a hypolophid. In all other features, M_3 resembles M_1 and M_2.

The lower incisor is rounded anteriorly. The cross-sectional shape of I_1 is roughly tear-drop shaped, relatively broad anteriorly and tapering to a point posteriorly. Enamel extends only slightly onto the medial and lateral sides of the incisor.

Discussion.—In his original description, Matthew (1918:618) provisionally referred this species to *Mysops,* an otherwise Bridgerian genus. He listed the type (AMNH 14731) and two referred specimens from the type area of the Lost Cabin Member of the Wind River Formation. Wilson (1937) pointed out that one of the referred specimens (AMNH 14729) did not belong to the same species as the type. Later, Dawson (1966) referred AMNH 14729 to *Microparamys lysitensis* which was later synonymized with *Knightomys depressus* (Guthrie, 1971). Several additional specimens, including those referred by Guthrie (1971) to "sciuravid cf. *Dawsonomys minor,*" have been recovered since Matthew's description.

Wilson (1937, 1949) considered "*Mysops*" *kalicola* a paramyine, and included it in his "*Paramys*" *buccatus* species group. Wood (1962) failed to discuss "*Mysops*" *kalicola* in his review of the Paramyidae because he did not consider it a paramyid. Dawson (1966:105) pointed out many similarities between "*Mysops*" *kalicola* and the Uintan species *Janimus rhinophilus* which, in turn, shared many similarities with early Oligocene *Eutypomys* from Texas. Black (1971) placed *Janimus* in the Reithroparamyinae in the Ischyromyidae but did not include "*Mysops*" *kalicola* in his classification. Guthrie (1971) included *Mysops kalicola* (without question marks) in the Sciuravidae without discussion.

Wood (1974) described a new primitive species of *Eutypomys, E. inexpectatus,* from the earliest Oligocene of Texas and compared it with *Janimus.* He included *Janimus* in the Microparamyinae (of the Paramyidae) rather than in the Eutypomyidae because of possible differences in the zygomasseteric structure but suggested that *Janimus* might represent a "collateral ancestor" (Wood, 1974:96). Later Dawson (1977:198) placed *Janimus* in "Family uncertain," stating ". . . this genus may be an early representative of the Eutypomyidae."

An undescribed isolated lower molar from the Duchesnian locality 20, Badwater Creek area, Wyoming (see Black and Dawson, 1966, for locality and age) is intermediate between *Janimus* and *E. inexpectatus* in size and morphology. This specimen supports the idea of a close relationship between *Janimus* and *Eutypomys.*

Mattimys kalicola has a number of similarities with *Janimus* (Dawson, 1966:105–106). The differences between *Mattimys* and *Janimus* are mostly primitive features in *Mattimys.* The hypolophid on M_2 of *Mattimys* runs the entire width of the tooth. In *Janimus* the hypolophid joins the posterolophid at its center. This may be the only feature in which *Mattimys* is more advanced than *Janimus.*

A single M^3 from the Bridger Formation (FMNH PM 15193), identified as *Microparamys* sp. B by West (1973), is comparable in size to *J. rhinophilus.* It has a number of prominent wrinkles in its central basin. These wrinkles are similar to those of the teeth of *Mattimys* and are not fine crenulations as in species of *Lophiparamys* and *Thisbemys.* This tooth probably belongs to either *Mattimys* or *Jan-*

imus, or represents an intermediate form between these two genera.

Because of possible differences in the zygomasseteric structure of *Janimus,* Wood (1974) suggested that it may represent an entirely different suborder, as well as family, from *Eutypomys.* The zygomasseteric structure of *Mattimys* is unknown but the position of the masseteric scar on the mandible does not differ from that of early ischyromyids, suggesting that no modification in the masseteric structure has occurred. Therefore, if *Mattimys* were included in the Eutypomyidae, the family would have members with both protrogomorphous and sciuromorphous zygomasseteric structures. This would also mean that sciuromorphy in this lineage was developed independently from other sciuromorphs. This is not a unique situation. Early sciurids (Black, 1963) do not have a completely sciuromorphous structure, but are clearly referable to the same family as the later fully sciuromorphous sciurids.

The union of *Mattimys, Janimus* and *Eutypomys* is based on the very strong similarity of their dentitions. Thus, both *Janimus* and *Mattimys* are here considered eutypomyids.

Two specimens from the Graybullian Four Mile fauna, an M_3 (UCMP 44103) and M_2 (UCMP 44104) were identified by McKenna (1960:84) as "?Subfamily Paramyinae, undescribed genus and species." He noted the similarity between these specimens and *Mattimys kalicola* but stated that there were significant differences, though he did not list them. The present location of these specimens is unknown (D. Savage and D. Guthrie, personal communication) but according to McKenna's (1960: Figs. 42a, b) figures, these specimens are very similar to M_2–M_3 of *Mattimys kalicola.* M_2 from the Four Mile fauna differs from that of *M. kalicola* in having wider trigonid than talonid, the metaconid obliquely compressed, and a less distinct hypolophid. In all other features this specimen is identical to M_2 of *M. kalicola.* The posterolophid of the Four Mile M_3 is not as strong as that of M_3 of *M. kalicola.* These specimens from the Four Mile fauna should be referred to *Mattimys,* without a specific identification.

CONCLUSIONS

Primitive Cranial and Dental Morphologies of Rodents

In the past, the origin of the rodents was believed to be found in Paleocene primates (Wood, 1962) or primitive "insectivores" (see Szalay, 1977:355–356). More recent discoveries of Paleocene mammals from the People's Republic of China have produced eurymyloids that show many resemblances to rodents, notably the late Paleocene eurymyloid *Heomys* (Li, 1977). These similarities led Hartenberger (1980) to suggest the origin of rodents from the Eurymyloidea (Li, 1977; =Mixodontia, Sych, 1971). Early Eocene ctenodactyloids from Asia such as "*Microparamys*" *lingchaensis* (Li et al., 1979) and *Tamquammys* (Shevyreva, 1971) share many dental features with *Heomys* (Dawson et al., in press) and support the idea of an Asian origin of rodents from a eurymyloid stock.

Traditionally, primitive ischyromyids (="paramyids" or "paramyines") have been viewed as the most primitive rodents that gave rise to all later rodents (for example, Wilson, 1949; Wood, 1962). However, with the recent evidence of early eurymyloids and ctenodactyloids from Asia, it appears that perhaps ctenodactyloids may represent the most primitive rodents (Dawson et al., in press) and the ischyromyids represent only the basal stock for certain later rodent groups.

Some of the dental fearures of *Heomys* that are also present in early ctenodactyloids (Dawson et al., in press) are: P^4 with single buccal cusp (paracone) and small, distinct hypocone; upper molars with well developed hypocone and metaloph directed anterolingually forming a "V" with the protoloph; P_4 with minute talonid; lower molars with large hypoconulid. All of these features are here considered primitive for rodents.

If the ctenodactyloids do indeed represent the primitive condition, the ischyromyids that are the most primitive are the reithroparamyines, which maintain a hypocone on P^4 and a distinct hypoconulid on the lower molars. The hypocones on the upper molars are relatively larger than in paramyines in reithroparamyines as well. The simpler pattern of the molars in paramyines would be more derived. *Reithroparamys ctenodactylops* maintains more primitive ctenodactyloid features than any other ischyromyid.

Wood (1962) viewed *Franimys amherstensis* from the Clarkforkian of the Bighorn Basin as the most primitive rodent. He believed that the primary buccal cusp on P^4 was the metacone and the paracone developed secondarily. This theory was based on a misinterpretation of the type specimen of *F. amherstensis* and does not seem likely in view of the recent discoveries of early ctenodactyloids from Asia.

Features of the skull and mandible that are considered to be primitive are: 1) nasal bones extend posteriorly to a level even with the posterior margin of the premaxillaries; 2) double mental foramen on the mandible; 3) posterior margin of the anterior root of the zygoma even with the posterior margin of P^4; 4) auditory bulla not ossified to the skull.

All reithroparamyines, pseudoparamyines, sciuravids, and early ctenodactyloids have the first feature listed above. The extent of the nasals and premaxillaries in *Heomys* is not known, but in several other eurymyloids the premaxillaries extend farther posteriorly than the nasals. In the Paramyinae, the nasals extend farther posteriorly than the premaxillaries, an obviously derived condition.

A double mental foramen on the mandible is present in *Heomys* and nearly all early ischyromyids and sciuravids. There is independent reduction to a single foramen several times.

The posterior margin of the anterior root of the zygoma in primitive mammals (such as insectivores, primates, and carnivores) is level with the posterior molars, and may even be farther posterior than M^3. In *Heomys*, it is level with the posterior margin of M^1. This continued forward movement of the zygoma is also present in rodents. The posterior margin of the anterior root of the zygoma in early ctenodactyloids and most paramyines is level with the posterior margin of P^4. In reithroparamyines it progressively moves forward until it is level with the anterior margin of P^4 in *Microparamys* and *Apatosciuravus*.

The anterior movement of the zygoma is accomplished independently in many lineages. In manitshines it moves forward, but not to the extent that it does in *Microparamys*. In two genera, *Mytonomys* and *Quadratomus*, the zygoma is more posterior. This is viewed as posterior movement from the primitive condition because these genera are otherwise quite derived and this feature is not present in any other members of their subfamilies of the Ischyromyidae.

It is consistent with nearly all other orders of early Tertiary mammals to suggest that the lack of a bony auditory bulla coossified with the skull is primitive for rodents. However, evidence from early species of rodents is rare and inconclusive. All Eocene ischyromyids except *Reithroparamys* (including "*Paramys*" *sciuroides*), for which basicranial material is preserved, lack a bulla ossified to the skull. Wood (1962) demonstrated that in some paramyines there is evidence that there was a bony bulla, but that it was not coossified with the skull. The earliest ctenodactyloid from Asia is known to preserve an ossified bulla at least loosely attached to the skull (Li, personal communication). All skulls of eurymyloids available to the author for study have bony auditory bullae ossified to the skull. The lack of a bony bulla coossified to the skull in rodents is here considered to be the primitive condition because of lack of any evidence to the contrary and the very poor evidence of the basicaraial region of early rodents.

Relationships of North American Paleocene and Early Eocene Rodents

Ischyromyidae

As stated above, the reithroparamyines represent the most primitive ischyromyids. The features that unite the reithroparamyines are the anterior position of the zygoma and masseter on the mandible and certain dental characters (discussed above). All paramyines can be derived from a primitive reithroparamyine stock by lengthening of the nasal bones of the skull and simplification of the occlusal pattern of the cheek teeth (Fig. 33). The most primitive paramyine is *Paramys taurus*, which possesses some of the primitive reithroparamyine characters, such as a hypoconulid on the lower molars and hypocone on P^4. These features are, however, reduced in *P. taurus* and continue to be more greatly reduced in later paramyines. The presence of an attached auditory bulla in reithroparamyines is considered an advanced character that might bar the Reithroparamyinae from ancestry of paramyines. However, this character is only known in middle and late Eocene species of reithroparamyines. Earliest species of reithroparamyines may not have possessed this character, and it was not developed in the Reithroparamyinae until after the Paramyinae had already split off.

Pseudoparamyines have an even simpler P^4 in their earliest forms, and can be readily derived from a paramyine stock.

The Paramyinae are well diversified in the late Eocene and a few genera persist into the early Oligocene (see Black, 1971; Wood, 1962, 1974; Storer, 1978). Wood (1962) and Black (1963) believed that the sciurids, which first appear in North America in the Oligocene, were possibly derived from the late Eocene paramyine *Uriscus*. This theory appears consistent with the trend in paramyines toward a simplification of the occlusal pattern of the dentition. It is also consistent with the derived features

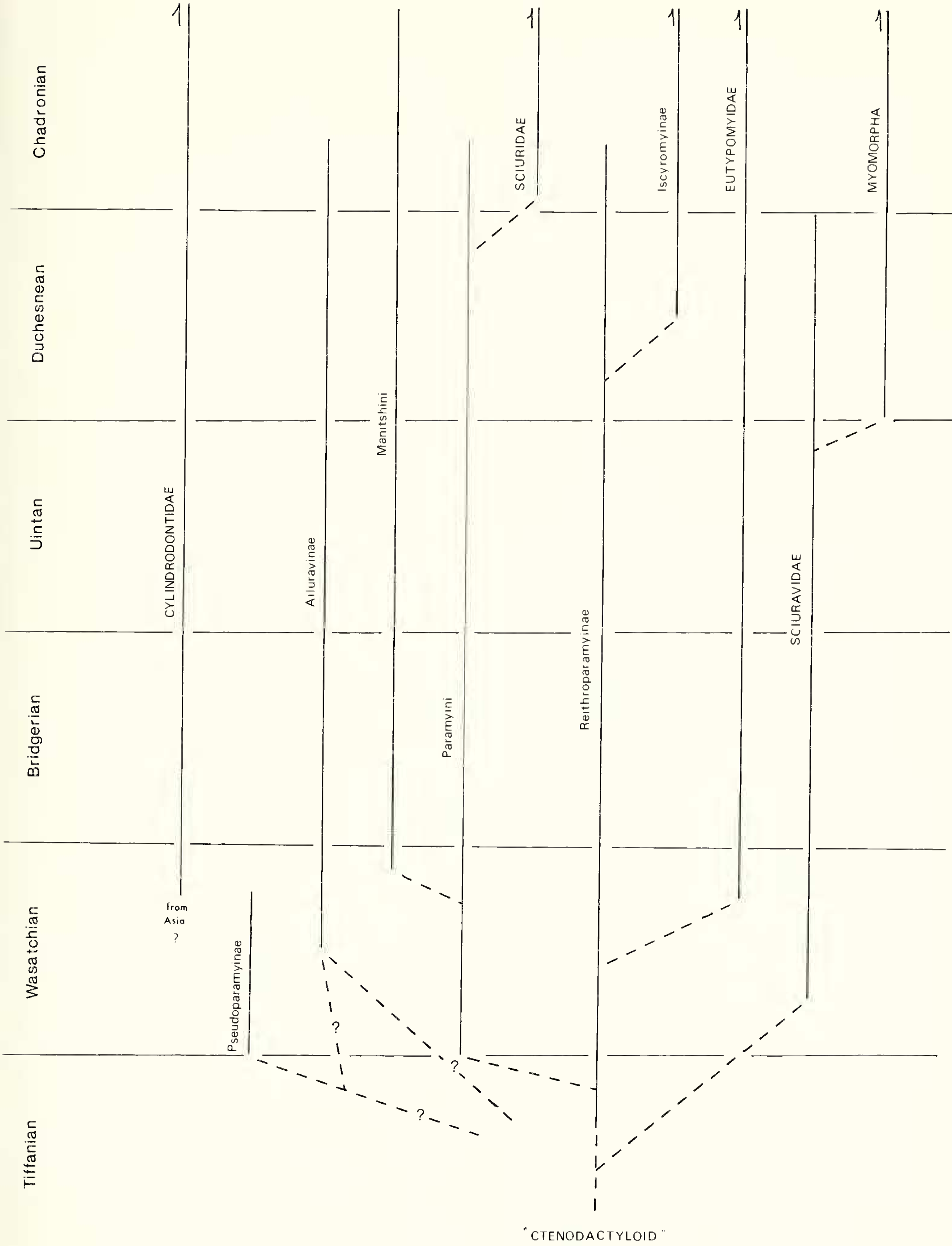


Fig. 33.—Proposed relationships of Eocene rodents in North America.

of the skulls of paramyines. The earliest sciurids have nasals that extend farther posterior than the premaxillaries (Black, 1963).

In several papers, both Wood (1962, 1976*a*) and Black (1968*a*, 1971) derived the Ischyromyinae (or Ischyromyidae) from the Paramyinae. The two genera that were suggested as possible ancestors to *Ischyromys* were *Leptotomus* and *Rapamys*. This phylogeny was based on dental characters. However, *Ischyromys* (including *Titanotheriomys* Matthew, 1910) maintains the primitive condition of its nasal bones which has been lost in paramyines. On this basis, ischyromyines cannot be derived from a paramyine.

Dentally, *Ischyromys* has a hypocone on P^4 and a relatively large hypocone on the upper molars. These too, do not follow the condition in *Leptotomus* or *Rapamys*, in which the upper dentition is simplified and the hypocones reduced or lost. Wahlert (1974) discounted the possibility of *Leptotomus* being an ancestor of *Ischyromys* on the basis of cranial foramina. The Eocene ischyromyid that is probably closest to representing an ancestral form for *Ischyromys* is *Reithroparamys*. The middle and late Eocene species of *Reithroparamys* develop lophs on their cheek teeth similar in arrangement to those of *Ischyromys*. P^4 of *Reithroparamys* is submolariform with a hypocone, also as in *Ischyromys*. Other features shared by these two genera are: 1) shorter, more tapered snout; 2) large bony auditory bulla fused to the skull; 3) anterior position of the anterior root of the zygoma; 4) masseteric fossa on the mandible marked by low ridges and terminating in a V-shape anteriorly; 5) double hypoglossal foramina; and 6) the presence of a post alar fissure on the skull. These features, and possibly the fusion of the scaphoid and lunar bones of the pes, relate these two genera. The dental pattern of *Ischyromys* can easily be derived from that of *Reithroparamys*. The only major difference between the Eocene *Reithroparamys* and the Oligocene *Ischyromys* is modification of the zygomassteric structure of the skull. In all the features of the skull that differ, *Reithroparamys* represents the primitive condition from which the skull of *Ischyromys* can be derived.

Both Matthew (1910) and Wilson (1949) derived the Sciuravidae from what they termed the "*Paramys buccatus* group." This group (with the exception of *Franimys buccatus* itself) is very near the Reithroparamyinae as accepted here. Dawson (1968*b*, 1974) suggested that the origin of the sciuravids was to be found at or near the origin of *Microparamys*. Wood (1962: Fig. 90) derived the sciuravids from the *Microparamys* line, but also derived *Sciuravus* alone directly from *Paramys francesi*. Sciuravids are most easily derived from an *Apatosciuravus*-like ancestor (see discussion below).

Microparamys is the most likely ancestor for *Mattimys kalicola* and the eutypomyids. The most convincing evidence is from the morphology of the anterior cingulum on the lower molars, which is unique to *Microparamys* and its supposed relatives. Wood (1962: Fig. 90) derived "*Mysops*" *kalicola* from *Lophiparamys*. The teeth of both *Mattimys* and *Lophiparamys* are derivable from a basic *Microparamys* pattern, although the types of complications formed on the teeth of the first two genera are entirely different from one another along with other differences in dental morphology (Dawson, 1966).

The Pseudoparamyinae are represented by a single genus, *Franimys*, in North America and do not persist beyond the middle early Eocene. There are no probable descendants of *Franimys* later in the Eocene. The Ailuravinae, likewise, are represented by *Mytonomys* only. This genus however, persisted into the late Eocene (Wood, 1956, 1962; Black, 1968*b*) and earliest Oligocene (Wood, 1974). *Mytonomys* does not appear to be related to any later North American rodent except perhaps *Eohaplomys* from the late Eocene which has some similarities to the European *Ailuravus*.

Sciuravidae

The Sciuravidae are an exclusively North American family of rodents (see Dawson, 1977). It has been suggested that sciuravids originated directly from *Microparamys* (Wood, 1962) or somewhere near the origin of *Microparamys* (Dawson, 1968*b*, 1974). While some features of *Microparamys*, such as a large hypocone on the upper molars and anterior position of the zygoma, are shared with sciuravids, the unique morphology of the anterior cingulum of the lower molars of *Microparamys* is not present in the earliest known species of the primitive sciuravid, *Knightomys*. Thus, sciuravids cannot be directly derived from *Microparamys*. The hypocone on the upper molars of *Microparamys* is relatively larger than in other ischyromyids, but is not as large relatively as those of sciuravids. If it were accepted that all rodents are derived from a ctenodactyloid-like ancestor, a large hypocone is the primitive condition for rodents and the *Microparamys* condition is derived over that of the sciuravids.

The hypocone on the upper molars of *Apatosci-*

uravus is larger than that of any species of *Microparamys*. There is no feature of the upper dentition of *Apatosciuravus* that would bar it from an ancestral position to the sciuravids. P^4 of *Apatosciuravus bifax* has a weakly formed metaloph and no distinct metacone, which is an intermediate condition between P^4 of early ctenodactyloids and the earliest sciuravids or ischyromyids. However, the morphology of the lower molars of *A. bifax* cannot be interpreted in the same way. There is no indication of a hypolophid in *A. bifax*, and the buccolingual compression of the trigonids of M_1–M_2 is not present in sciuravids. If, however, *A. bifax* represents the most primitive sciuravid, the morphology of P^4 of this species would indicate a derivation of sciuravids from a ctenodactyloid ancestor separate from that of ischyromyids.

The earliest definite sciuravid is *Knightomys* from the early Eocene. The dental pattern of all Bridgerian and later sciuravids can be easily derived from that of *Knightomys*. Though the last sciuravids occur in the late Eocene, they have been long considered in the ancestry of later geomyoid and myomorph rodents (Wood, 1937; Wilson, 1949; Dawson, 1977).

Eutypomyidae

Mattimys kalicola is here believed to represent the earliest eutypomyid. It can be derived from *Microparamys* on the basis of dental morphology. Wood (1962) suggested that *M. kalicola* arose from *Lophiparamys*. However, *Lophiparamys* is already too specialized along its own line to have produced the molar morphology of *Mattimys*.

There is no indication that the zygomasseteric structure of *Mattimys* was advanced beyond the primitive protrogomorphous condition, unlike the Oligocene eutypomyids, which are sciuromorphous. The strong dental similarity of *Mattimys*, the late Eocene *Janimus*, and Oligocene *Eutypomys* makes the exclusion of the Eocene genera from the Eutypomyidae unlikely. If the zygomasseteric structure of the Eocene genera were viewed as having supergeneric significance, *Mattimys* and *Janimus* could well represent a primitive subfamily of the Eutypomyidae.

Cylindrodontidae

Wilson (1949) viewed the earliest cylindrodont, *Mysops*, from the middle Eocene, as originating from a primitive paramyine stock (=Paramyidae, *sensu* Wood, 1962). *Dawsonomys*, from the early Eocene, shares many cylindrodont characters and may represent the earliest known taxon of the family (see above discussion of *Dawsonomys*).

The cheek tooth pattern of *Dawsonomys* is not readily derivable from that of any early ischyromyid or sciuravid. It has some similarities with early Asian ctenodactyloids, such as the morphology of the trigonids of P_4 and M_1. *Dawsonomys* may have some relationship with the early Asian ctenodactyloids, but is too poorly known to suggest more than a possible relationship.

Occurrence and Radiation of Rodents in the Paleocene and Early Eocene of North America

The earliest occurrence of rodents in the world is still that of *Acritoparamys atavus* from the unique Tiffanian Bear Creek fauna of Montana. One of the unique features of this fauna is the lack of miltituberculates (see Krause, 1980). Van Valen and Sloan (1966) suggested that the early radiation of rodents in the Eocene was a major factor in the extinction of the multituberculates due to competition between these groups of animals. It is difficult to believe that the presence of a single species of rodent could have out-competed all of the multituberculates at this locality when multituberculates were still surviving elsewhere. Competition from rodents may have aided in the extinction of multituberculates, but multituberculates were already declining by the time of the first appearance of rodents.

By the earliest Eocene, ischyromyids were well diversified in both North America and Europe. Four genera, representing three different subfamilies, are present in the Clarkforkian level in the Bighorn Basin: *Paramys* (Paramyinae), *Acritoparamys* and *Apatosciuravus* (Reithroparamyinae), and *Franimys* (Pseudoparamyinae). Godinot (1981) reported three genera of three different subfamilies of ischyromyids from what he believed was equivalent in age to the Clarkforkian of France—*Paramys* (Paramyinae), *Microparamys* (Reithroparamyinae), and an indeterminate ailuravine. This clearly demonstrates the very rapid radiation of rodents at this time. There is very little difference between the Graybullian rodents and those from what has been called the Clarkforkian of the Bighorn Basin. All of the commonly occurring species of the Graybullian, *Paramys taurus*, *Apatosciuravus bifax*, and *Acritoparamys atwateri*, are also present in the Clarkforkian. *Paramys copei* is also present at both levels but rare. The only species that are exclusive to either level are all known by single specimens. From the Clarkforkian, *Fran-*

imys amherstensis is only known from the holotype and is not present in any Graybullian faunas. *Lophiparamys murinus, Microparamys scopaiodon* and an indeterminate reithroparamyine are represented in the Graybullian, also by single specimens. The lack of these Graybullian species in the Clarkforkian beds may be due to collecting error because all of these species are very small and may have been overlooked. The differences in the rodent faunas from the Graybullian and Clarkforkian are less than those between any of the subsequent subdivisions of the Wasatchian, suggesting that the Clarkforkian (according to the rodents) may represent the lower Graybullian of Van Houten (1945).

By Lysitean times, sciuravids become a significant part of the rodent fauna, represented by two species, *Knightomys minor* and *K. depressus.* During this time, and through the Gardnerbuttean, small reithroparamyines that were common in the Graybullian, such as *Apatosciuravus* and *Microparamys,* are rare. This lack of small ischyromyids may be due to competition from the abundant small sciuravids.

Ischyromyids begin to diversify in the Lysitean and the common species in the Graybullian, *Paramys taurus* and *Acritoparamys atwateri* disappear and *P. copei* and *P. excavatus* replace them as the dominant species. The Lysitean rodent fauna is relatively uniform throughout North America. Only a few rare species, such as *Notoparamys arctios, Franimys ambos,* and *Thisbemys* sp., are not present in all Lysitean faunas.

In the late Wasatchian, the sciuravids become quite diverse. The first appearance of *Pauromys, Sciuravus,* and two more species of *Knightomys* occurs in the Lostcabinian along with the continuation of *K. depressus* from the Lysitean. Along with the sciuravids, it is also the first appearance of the ?eutypomyid *Mattimys* and ?cylindrodontid *Dawsonomys.* Ischyromyids, however, do not undergo as rapid a radiation as the sciuravids, but show some regional variation. *Notoparamys costilloi, Thisbemys perditus, Acritoparamys pattersoni,* and *Paramys nini* are known from faunas in Colorado and New Mexico but not Wyoming. *Acritoparamys francesi* is common in the Wyoming faunas and unknown from the more southern areas. This regional differentiation might indicate a shift from a more uniform environment throughout western North America during the middle Wasatchian to more regionally restricted environments in the late Wasatchian.

The Gardnerbuttean is marked by a continuation of most Lostcabinian species, introduction of a few genera and species that continue into the Bridgerian, such as *Quadratomus, Leptotomus,* and *Reithroparamys huerfanensis,* and disappearance of some earlier forms, such as *Notoparamys* and *Paramys excavatus.* In the Bridgerian, there is an almost complete replacement of all Wasatchian species. Large manitshines and paramyines are common and sciuravids become even more diverse.

Only one species of rodent is common throughout the early Eocene, *Paramys copei. Paramys copei* is represented in all faunas from the Clarkforkian through the Gardnerbuttean, and would best serve as an index fossil for the Wasatchian (?and Clarkforkian) of North America.

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LITERATURE CITED

Alston, E. R. 1876. On the classification of the order Glires. Proc. Zool. Soc. London, 1876:61–98.

Black, C. C. 1963. A review of the North American Tertiary Scirridae. Bull. Mus. Comp. Zool., 130:109–248.

———. 1968*a*. The Oligocene rodent *Ischyromys* and discussion of the family Ischyromyidae. Ann. Carnegie Mus., 39: 273–305.

———. 1968*b*. The Uintan rodent *Mytomonmys*. J. Paleontol., 42:853–856.

———. 1971. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 7. Rodents of the family Ischyromyidae. Ann. Carnegie Mus., 43:179–217.

Black, C. C., and M. R. Dawson. 1966. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 1, History of field work and geological setting. Ann. Carnegie Mus., 38:297–307.

Black, C. C., and J. J. Stephens III. 1973. Rodents from the Paleogene at Guanajuato, Mexico. Occas. Papers Mus., Texas Tech Univ., 14:1–10.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. J. Smith, Paris, 115 pp.

Brandt, J. F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. Mém. Acad. Imp. Sci., Pétersbourg, ser. 6, 9:1–375.

Bravard, A. 1850. Pp. 2–3, *in* P. Gervais. Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France. Paris, Vol. 2, 128 pp.

Cope, E. D. 1872. Second account of new Vertebrata from the Bridger Eocene. Proc. Amer. Phil. Soc., 12:466–468.

———. 1873. On some Eocene mammals obtained by Hayden's geological survey of 1872. Palaeont. Bull., 12:1–6.

———. 1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Rept. U.S. Geogr. Surv. West of 100th Merid., 4 (pt. 2):1–370.

———. 1884. The Vertebrata of the Tertiary formations of the West. Rept. U.S. Geol. Surv. Terr., 3:1–1009.

Dawson, M. R. 1966. Additional late Eocene rodents (Mammalia) from the Uinta Basin, Utah. Ann. Carnegie Mus., 38: 97–114.

———. 1968*a*. Oligocene rodents (Mammalia) from East Mesa, Inner Mongolia. Amer. Mus. Novit., 2324:1–12.

———. 1968*b*. Middle Eocene rodents (Mammalia) from northeastern Utah. Ann. Carnegie Mus., 39:327–370.

———. 1974. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 8. The rodent *Microparamys* (Mammalia). Ann. Carnegie Mus., 45:145–150.

———. 1977. Late Eocene rodent radiations: North America, Europe and Asia. Geobios, Mém. Spec., 1:195–209.

Dawson, M. R., Li C. K., and Qi T. (in press). Eocene ctenodactyloid rodents (Mammalia) of eastern and central Asia. Bull. Carnegie Mus.

Ferrusquia-Villafranca, I., and A. E. Wood. 1969. New fossil rodents from the early Oligocene Rancho Gaitan local fauna, northeastern Chihuahua, Mexico. Texas Mem. Mus., Pearce-Sellards Series, 16:1–13.

Gazin, C. L. 1952. The Lower Eocene Knight Formation of western Wyoming and its mammalian faunas. Smithsonian Misc. Coll., 117:1–82.

———. 1961. New sciuravid rodents from the Lower Eocene Knight Formation of western Wyoming. Proc. Biol. Soc. Washington, 74:193–194.

———. 1962. A further study of the Lower Eocene mammalian faunas of southwestern Wyoming. Smithsonian Misc. Coll., 144:1–98.

Gingerich, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Paper Paleon., Univ. Michigan, 15:1–141.

Gingerich, P. D., K. D. Rose, and D. W. Krause. 1980 Early Cenozoic mammalian faunas of the Clark's Fork Basin-Polecat Bench area, northwestern Wyoming. Pp. 51–68, *in* Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming (P. D. Gingerich, ed.), Papers Paleon., Univ. Michigan, 24:51–68.

Godinot, M. 1981. Les mammifères de Rians (Eocène Inférieur, Provence). Palaeovertebrata, 10:43–126.

Granger, W. 1910. Tertiary faunal horizons in the Wind River Basin, Wyoming, with descriptions of new Eocene mammals. Bull. Amer. Mus. Nat. Hist., 28:235–251.

———. 1914. On the names of Lower Eocene faunal horizons of Wyoming and New Mexico. Bull. Amer. Mus. Nat. Hist., 33:201–207.

Guthrie, D. A. 1967. The mammalian fauna of the Lysite Member, Wind River Formation (early Eocene) of Wyoming. Mem. So. California Acad. Sci., 5:1–52.

———. 1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (Lower Eocene) of Wyoming. Ann. Carnegie Mus., 43:47–113.

Hartenberger, J.-L. 1980. Données et hypotheses sur la radiation initiale des rongeurs. Palaeovertebrata, Mém Jub. en homm. à R. Lavocat, pp. 285–302.

Jepsen, G. L. 1937. A Paleocene rodent, *Paramys atavus*. Proc. Amer. Phil. Soc., 78:291–301.

Kelley, D. R., and A. E. Wood. 1954. The Eocene mammals from the Lysite Member, Wind River Formation of Wyoming. J. Paleontol., 28:337–366.

Korth, W. W. 1980. *Paradjidaumo* (Eomyidae, Rodentia) from the Brule Formation, Nebraska. J. Paleontol., 54:933–941.

Krause, D. W. 1980. Multituberculates from the Clarkforkian land-mammal age, late Paleocene-early Eocene of western North America. J. Paleontol., 54:1163–1183.

Landry, S. O. 1957. The interrelationships of the New and Old World hystricomorph rodents. Univ. California Publ. Zool., 56:1–118.

Leidy, J. 1871. Notice of some extinct rodents. Proc. Acad. Nat. Sci. Philadelphia, 22:230–232.

Li C. K. 1977. Paleocene eurymyloids (Anagalida, Mammalia) of Qianshan, Anhui. Vert. PalAsiat., 15:103–118 (in Chinese).

Li C. K., Chiu C. S., Yan D. F., and Hsieh S. H. 1979. Notes on some early Eocene mammalian fossils of Hengtung, Hunan. Vert. PalAsiat., 17:71–82 (in Chinese).

Loomis, F. B. 1907. Wasatch and Wind River rodents. Amer. J. Sci., ser. 4, 23:123–130.

Marsh, O. C. 1871. Notice of some new fossil mammals and birds from the Tertiary formation of the West. Amer. J. Sci., ser. 3, 2:120–127.

———. 1872. Preliminary description of new Tertiary mammals. Amer. J. Sci., ser. 3, 4:202–224.

Matthew, W. D. 1909. Faunal lists of the Tertiary Mammalia of the West. U.S. Geol. Surv. Bull., 361:91–138.

———. 1910. On the osteology and relationships of *Paramys* and the affinities of the Ischyromyidae. Bull. Amer. Mus. Nat. Hist., 28:43–71.

———. 1918. A revision of the Lower Eocene Wasatch and Wind River faunas. Pt. 5. Insectivora (continued), Glires, Edentates. Bull. Amer. Mus. Nat. Hist., 38:565–657.

———. 1920. A new genus of rodents from the middle Eocene. J. Mamm., 1:168–169.

McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. California Publ. Geol. Sci., 37:1–130.

———. 1961. A note on the origin of rodents. Amer. Mus. Novit., 2037:1–5.

Michaux, J. 1964. Diagnoses de quelques Paramyidés de l'Eocène inférieur de France. C. R. Somm. Soc. Géol. Fr., 1964 (4):153.

———. 1968. Les Paramyidae (Rodentia) de l'Eocène inférieur du Bassin de Paris. Palaeovertebrata, 1:135–193.

Miller, G. S., Jr., and J. W. Gidley. 1918. Synopsis of the supergeneric groups of rodents. J. Washington Acad. Sci., 8: 431–448.

Peterson, O. A. 1919. Report upon the material discovered in the Upper Eocene of the Uinta Basin by Earl Douglass in the years 1908–1909 and by O. A. Peterson in 1912. Ann. Carnegie Mus., 12:40–168.

Rensberger, J. M. 1975. *Haplomys* and its bearing on the origin of the aplodontid rodents. J. Mamm., 56:1–14.

Robinson, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene of Colorado. Bull. Peabody Mus. Nat. Hist., 21:1–95.

Roger, O. 1896. Verzeichniss der bisher bekannten fossilen Säugethiere. Neu zusammengestellt von Dr. Roger, kgl. Regierungs-und Kreis-Medizinrath in Augsburg. Bericht des Naturwiss. Vereins für Schwaben und Neuburg (a.V.), 32:1–272.

Rose, K. D. 1975. The Carpolestidae. Early Tertiary primates from North America. Bull. Mus. Comp. Zool., 147:1–74.

———. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. Papers Paleon., Univ. Michigan, 26:1–196.

Rütimeyer, C. L. 1891. Die Eocäne Säugethier-Welt von Egerkingen. Gesammtdarstellung und dritter Nachtrag zu den "Eocänen Säugethieren aus dem Gebiet des schweizerischen Jura (1862)." Abhand. Schweizer. Palaeont. Gesell., 18:1–153.

Scott, W. B. 1895. *Protoptychus hatcheri*, a new rodent from the Uinta Eocene. Proc. Adad. Nat. Sci. Philadelphia, 47: 269–286.

Scott, W. B., and H. E. Osborn. 1887. Preliminary report on the vertebrate fossils of the Uinta formation, collected by the aprinceton Expedition of 1886. Proc. Amer. Phil. Soc. 24:255–264.

Shevyreva, N. S. 1971. The first find of Eocene rodents in the USSR. Bull. Acad. Sci. Georgian S. S. R., Tbilissi, 61:745–747 (in Russian).

Simpson, G. G. 1928. A new mammalian fauna from the Fort Union of southern Montana. Amer. Mus. Novit., 297:1–15.

———. 1929*a*. A collection of Paleocene mammals from Bear Creek, Montana. Ann. Carnegie Mus., 19:115–122.

———. 1929*b*. Third contribution to the Fort Union fauna at Bear Creek, Montana. Amer. Mus. Novit., 345:1–12.

———. 1941*a*. A giant rodent from the Oligocene. Science, 93: 474–475.

———. 1941*b*. A giant rodent from the Oligocene of South Dakota. Amer. Mus. Novit., 1149:1–16.

———. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., 85:1–350.

———. 1948. The Eocene of the San Juan Basin, New Mexico. Part 2. Amer. J. Sci., 246:363–385.

Stock, C. 1935. New genus of rodents from the Sespe Eocene. Bull. Geol. Soc. Amer., 46:61–68.

Storer, J. E. 1978. Rodents of the Calf Creek local fauna (Cypress Hills Formation, Oligocene, Chadronian), Saskatchewan. Saskatchewan Mus. Nat. Hist. Contrib., 1:1–54.

Stucky, R., and L. Krishtalka. 1982. Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 1. Introduction and Multituberculata. Ann. Carnegie Mus., 51: 39–56.

Sych, L. 1971. Mixodontia, a new order of mammals from the Paleocene of Mongolia. Palaeontol. Polonica, 25:147–158.

Szalay, F. S. 1977. Phylogenetic relationships and a classification of the eutherian Mammalia. Pp. 315–374 *in* Major patterns in vertebrate evolution (M. K. Heckt, P. C. Goody, and B. M. Heckt, eds.), Plenum Press, New York, 908 pp.

Troxell, E. L. 1923. *Pauromys perditus*, a small rodent. Amer. J. Sci., 5:155–156.

Tullberg, T. 1899. Ueberdas System der Nagethiere: eine phylogenetische Studie. Nova Acta Reg. Soc. Sci. Upsala, 18:1–514.

Van Houten, F. B. 1945. Review of latest Paleocene and early Eocene mammalian faunas. J. Paleontol., 19:421–461.

Van Valen, L., and R. E. Sloan. 1966. The extinction of the multituberculates. Syst. Zool., 15:261–278.

Wahlert, J. H. 1973. *Protoptychus*, a hystricomorphous rodent from the late Eocene of North America. Breviora, 419:1–14.

———. 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bull. Mus. Comp. Zool., 146:363–410.

Weitzel, K. 1949. Neue Wirbeltiere (Rodentia, Insectivora, Testudinata) aus dem Mitteleozän von Messel bei Darmstadt. Abhand. senckenbergishen naturf. Gesell., 480:1–24.

West, R. M. 1969. *Paramys wyomingensis*, a small rodent from the middle Eocene of Wyoming. J. Paleontol., 43:175–178.

———. 1973. Geology and mammalian paleontology of the New Fork-Big Sandy area, Sublette County, Wyoming. Fieldiana: Geology, 29:1–193.

Wilson, R. W. 1937. Two new Eocene rodents from the Green River Basin, Wyoming. Amer. J. Sci., ser. 5, 34:447–456.

———. 1938. Review of some rodent genera from the Bridger Eocene. Amer. J. Sci., ser. 5, 35:123–137.

———. 1940. Californian paramyid rodents. Carnegie Inst. Washington Publ., 514:59–83.

———. 1949. Early Tertiary rodents of North America. Carnegie Inst. Washington Publ., 584:59–83.

Wood, A. E. 1937. The mammalian fauna of the White River Oligocene. Pt. II, Rodentia. Trans. Amer. Phil. Soc., 28:155–269.

———. 1955. A revised classification of the rodents. J. Mamm., 36:165–187.

———. 1956. *Mytonomys,* a new genus of paramyid rodent from the Upper Eocene. J. Paleontol., 30:753–755.

———. 1958. Are there rodent suborders? Syst. Zool., 7:169–173.

———. 1959*a.* Rodentia. *In* The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming (P. O. McGrew), Bull. Amer. Mus. Nat. Hist., 117:157–169.

———. 1959*b.* A new sciuravid rodent of the genus *Pauromys* from the Eocene of Wyoming. Amer. Mus. Novit., 1978: 1–6.

———. 1962. The early Tertiary rodents of the family Paramyidae. Trans. Amer. Phil. Soc., 52:1–261.

———. 1965. Small rodents from the early Eocene Lysite Member, Wind River Formation of Wyoming. J. Paleontol., 39: 124–134.

———. 1970. The European Eocene paramyid rodent, *Plesiarctomys.* Verhandl. Naturf. Gesell. Basel, 80:237–278.

———. 1972. An Eocene hystricognathous rodent from Texas: its significance in interpretations of continental drift. Science, 175:1250–1251.

———. 1973. Eocene rodents, Pruett Formation, southwest Texas; their pertinence to the origin of the South American Caviomorpha. Pearce-Sellards Ser., Texas Mem. Mus., 20: 1–40.

———. 1974. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Rodentia. Bull. Texas Mem. Mus., 21: 1–112.

———. 1975. The problem of hystricognathous rodents. Papers Paleon., Univ. Michigan, 12:75–80.

———. 1976*a.* The Oligocene rodents *Ischyromys* and *Titanotheriomys* and the content of the family Ischyromyidae. Pp. 244–277, *in* Athlon: essays on paleontology in honour of L. S. Russell (C. S. Churcher, ed.), Univ. Toronto Press, Toronto, 277 pp.

———. 1976*b.* The paramyid rodent *Ailuravus* from the middle and late Eocene of Europe, and its relationships. Paleovertebrata, 7:117–149.

———. 1980. The Oligocene rodents of North America. Trans. Amer. Phil. Soc., 70:1–68.

———. 1981. The origin of the caviomorph rodents from a source in Middle America: A clue to the area of origin of the platyrhine primates. Pp. 79–91, *in* Evolutionary biology of the New World monkeys and continental drift (R. L. Ciochon and A. B. Chiarelli, eds.), Plenum Publ. Corp., New York, 528 pp.

Wood, A. E., and R. W. Wilson. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. J. Paleontol., 10:388–391.

Wood, H. E., II, R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Amer., 52:1–48.

Woods, C. A. 1972. Comparative myology of jaw, hyoid and pectoral appendicular regions of New and Old World hystricomorph rodents. Bull. Amer. Mus. Nat. Hist., 147:117–198.

Zittle, K. A. von. 1893. Handbuch der Palaeontologie. I. Abth. Palaeozoologie. Iv. Band. Vertebrata (Mammalia), Munich and Leipzig, 799 pp.